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VOLUME 16, No. 2 NOVEMBER 1947

A NEW MODIFICATION OF THE TULLGREN APPARATUS

BY NIELS HAARLØV, *The Zoological Museum of Copenhagen*

(With 6 Figures in the Text)

Trägårdh & Forsslund (1932), in their fundamental work on the effectiveness of the Tullgren apparatus, showed how the desiccation methods for driving out animals from the soil should be modified according to the nature of the habitat. When in 1942 I began an investigation into the Collembolan and Acarine fauna in the soil from localities as different as commons, forest soil and lake banks, my first task was to construct a Tullgren apparatus which was so adaptable in operation that it could be used in all three habitats. The result was the box shown in Fig. 1. After completion of my investigations this Tullgren apparatus was also employed by other investigators of Collembola and Acarina in Denmark and with earth samples from highly different localities.

It is not possible to be precise about the reliability of these results, since the animals are too small to be collected directly; I shall therefore only give an account of the construction of the apparatus and of some of the results which I have so far obtained by means of it.

The construction of my Tullgren apparatus will be clear from Fig. 1. The bulb is a carbon incandescent lamp whose point is placed at a distance of 15 cm. from the wire-netting, the funnel is a glass one and the walls of the box consist of 8 mm. thick plywood.

The apparatus has been used in the following way. First the earth sample (0·001 sq.m., 6–7 cm. deep) was taken to pieces and placed on the wire-netting so that it formed a uniform layer about 2 cm. high which *nowhere* reached to the border of the netting. Then the lamp was lighted and the lid closed more or less: the moister the sample the larger was the opening, since then the air circulation and therefore the evaporation from the surface of the sample would be more effective. After 6–12 hr.—the period varying according to the size and water content of the sample—the lamp was replaced by a stronger one and the lid was closed. From this moment until no more animals could be driven out of the sample no changes were made in the arrangement of the apparatus.

The sorting out of the animals was made at first with a magnification of 10 × and then with one of 30 ×. From (1) forest soil, (2) commons, and (3) north- and (4) south-exposed sides of 'ant hillocks' on the commons respectively, I have found as average figures per sample for 26 samples in the period 30 April 1942–17 May 1943 the following aggregate numbers of Collembola and Acarina: 338, 288, 426, 275.

In order to get an impression of the mode of action of the apparatus I made five experiments with forest soil which all gave the same type of result and which I shall, therefore, discuss collectively, illustrated by Figs. 2–6 and Tables 2–6.

The experiments were made to measure the fluctuations in the temperature and relative humidity (R.H.) of the earth samples during desiccation and correlate them with the times when the different species of Collembola and Acarina emigrated from the samples.

The temperature was measured with a tube thermometer $-17°$ to $+60°$ C. (with a bulb 14 mm. long and 5 mm. broad, containing mercury) partly just outside the earth sample, where the bulb was covered with a layer of tinfoil, and partly in the earth sample proper 0·5–1 cm. at the lower end.

The R.H. of the air was measured by the Nielsen-Thamdrup method (1939), according to which the R.H. of the surrounding air can be directly measured from the position of the meniscus in small capillaries filled with sulphuric acid of a certain dilution. In all the experiments the air humidity was measured in the lowermost cm. of the earth sample, and in three of them also 0·5–0·25 cm. above the surface of the sample itself. The first measurements should be regarded as the result of influences partly from the air humidity in the lowermost layer of the sample proper, partly from the air humidity in the free air layer just below the under side of the sample.

The times for the expulsion of the animals were checked by changing the collecting glasses each hour until the air humidity of the earth sample had reached its minimum value. After that time several hours generally passed between each change. Altogether 3035 animals were expelled from the five earth samples examined.

During the first 6 hr. of the experiments the boxes were only half closed and illumination was made by means of a 10 W. carbon incandescent lamp; during the rest of the experiments the lids were firmly closed and a 15 W. incandescent lamp was used.

The air humidity and the temperature inside the samples naturally reach their minimum and maximum values respectively at the same time (Figs. 2, 3). In the three other experiments (not figured here) the average R.H. before it began to fall was about 95–100% in the lowermost layer instead of 90–95%. The fluctuations in humidity on the upper and under sides of the sample (Fig. 2) differ too much to indicate the humidity conditions in the mid-layer. A priori I believe that they would rather follow the curve for the under layer than for the upper. In the three other experiments in which the surface humidity was measured it did not drop further than the humidity inside the earth sample, i.e. about 30–25% R.H. at the end of the experiment.

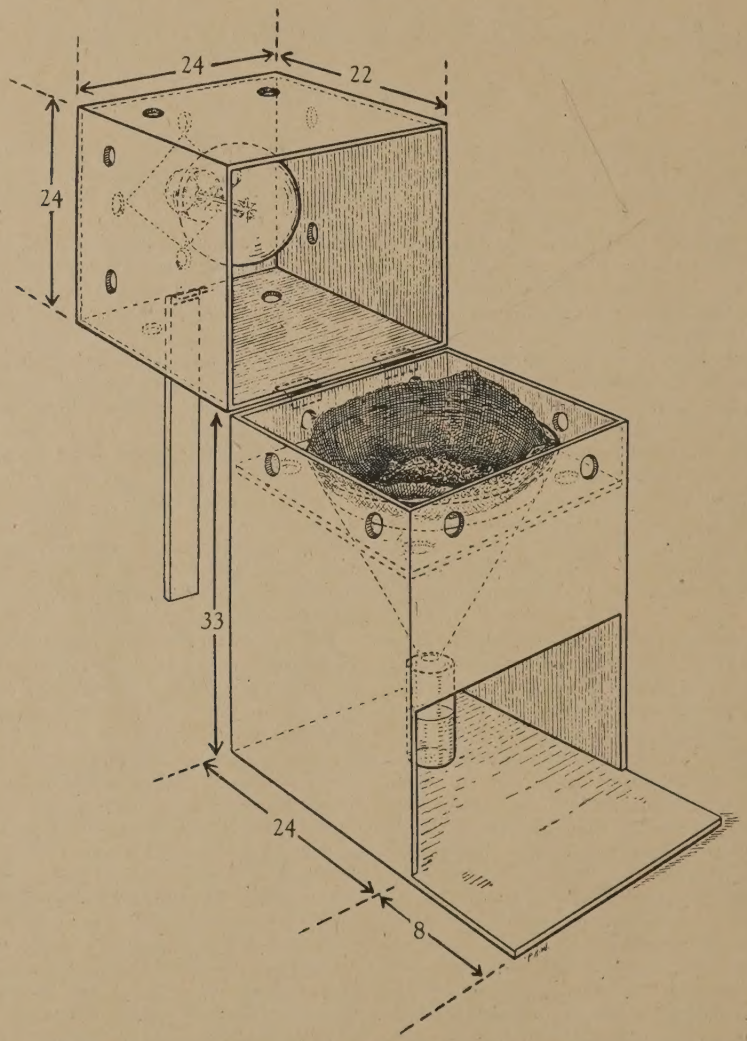

Fig. 1. The Tullgren apparatus employed (after Thorson, 1946). All measurements in cm.

The figures clearly show how the times at which the animals leave the samples are affected by the major changes in temperature and humidity. This is most

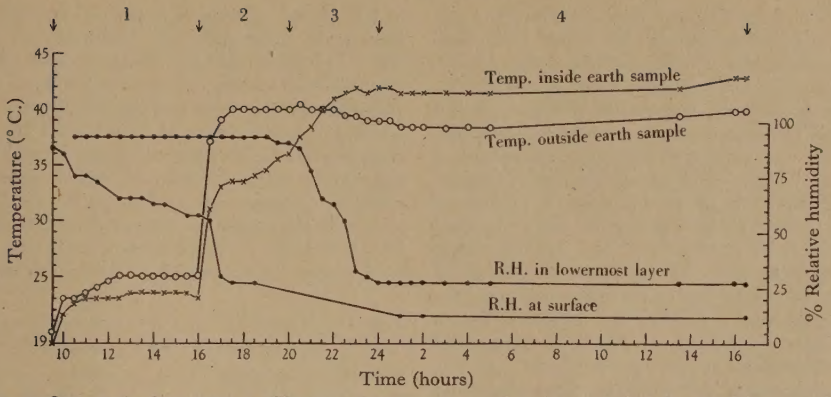

Fig. 2. 13 Oct. 1946. Apparatus 1. Changes of temperature and moisture during the expulsion experiment.

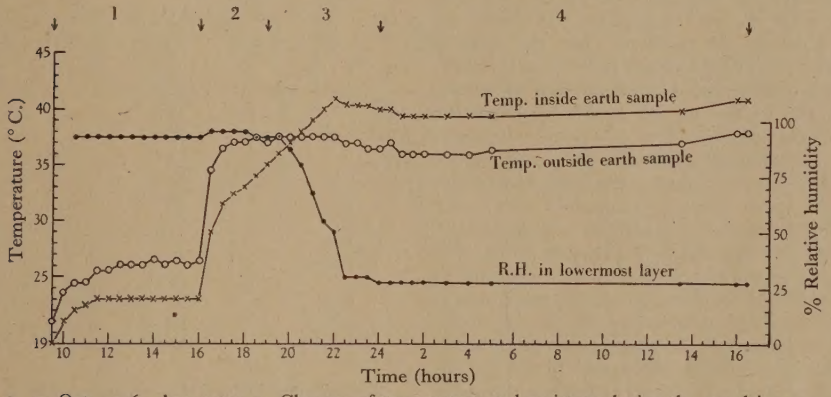

Fig. 3. 13 Oct. 1946. Apparatus 2. Changes of temperature and moisture during the expulsion experiment.

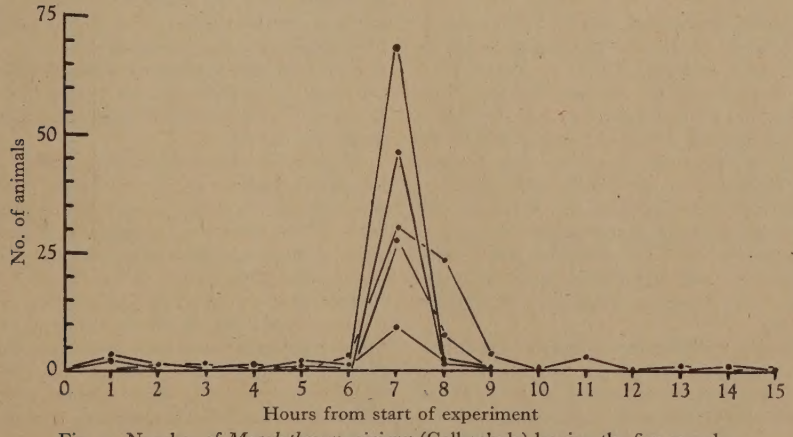

Fig. 4. Number of *Megalothorax minimus* (Collembola) leaving the five samples.

evident for *Megalothorax minimus* (Willem) (cf. Fig. 4), in which practically the whole emigration takes place immediately after the lid has been closed, and the heavy rise of temperature has occurred.

Figs. 5–6 show the emigration of the combined numbers of Collembola and Acarina per sample, and, between the sixth and eighth hour, the total number of animals minus the number of emigrated *Megalothorax minimus*. The emigration seems to be divided into four phases: (1) The first 6 hr., the emigration being greatest during the first hour, and decreasing during the following 5 hr. (2) From the change of temperature in the seventh hour to the time when the air in the lowermost layer of the sample is falling through about 90 % R.H. (3) The drop from about 90 % to the minimum value 30–25 % R.H. (4) The last part of the experiment where the temperature and humidity in the samples are fairly constant.

This division into four phases I shall try to explain as follows: The maximum in phase 1 is due to the animals which at the moment when the lamp is lighted are to be found in small isolated earth lumps on the wire-netting: these lumps are rapidly heated, dried and left by the animals which fall down the funnel. In the interior of the main sample there are, however, not sufficiently great changes of temperature and air humidity to cause a large-scale emigration. The maximum in phase 2 is certainly due to the change of temperature in the seventh hour and should be regarded as a reaction by flight against this. The air humidity in the sample is, however, constant or shows even a faint tendency to rise. The maximum in phase 3 is no doubt correlated with the fall of the humidity in the sample. In phase 4 the emigration is but small, either because practically all the animals have been expelled at this time, or because they have been killed by the low humidity before they managed to get out.

In order to elucidate the reaction of 'thick-skinned' and 'thin-skinned' Acarina to fluctuations in the air humidity I have included Table 1. Trägårdh & Forsslund (1932) are of the opinion that the 'thin-skinned' ones are more sensitive to low degrees of humidity than are the 'thick-skinned'. But in the first place, these two categories are certainly artificial and hardly form physiological units, although they have certain morphological common features; and secondly, my figures for *Notaspis coleoptratus* L. and *Platynotrus peltifer* C. L. Koch show that 'thin-skinned' nymphs and larvae and 'thick-skinned' adults leave the samples gradually throughout phases 2 and 3.

The most important source of error of the apparatus is, in my opinion, the possible formation of dew on the inner side of the funnel, this may, however, be *completely* avoided by taking the measures mentioned on p. 115. Another point of uncertainty lies in the size of the sudden change of temperature. The sudden large-scale emigration of *Megalothorax minimus* seems to indicate that the change of temperature has almost acted as a temperature shock to these animals. It might therefore seem probable that to other species which are less resistant to temperature the sudden change might have a paralysing effect so that they did not get time to leave the sample. Strictly speaking, the maximum temperature in the samples should never rise above the maximum temperature of the localities investigated (for the localities mentioned on p. 115 this would mean 20, 27, 29 and 44° C. respectively).

Table 1. *Numbers of Acarina—adults (a), nymphs (n) and larvae (l)—leaving the samples*

Notaspis coleoptratus Apparatus					*Platynotrus peltifer* Apparatus			
1			2			1		2
a	*n*	*l*	*a*	*n*	*l*	13 Oct. 46 Time	*a*	*n*	*l*	*a*	*n*	*l*
		1			3	11.00	2	1			—	
		—			1	12.00			1	1	1	
		—	2	1		13.00	1	1			3	
		—			—	14.00	1				—	
1					—	15.00		—			—	
		—			—	16.00		—			—	
5	6		3	2		17.00	3	6	2	2	5	2
4	3	2	1	4	2	18.00	2	1		1	1	1
1	4	3	1	1	1	19.00	2	3	2	3	6	
	1	1		7	1	20.00	2	5	1	1	7	5
	2			7		21.00	2	4	2	4	11	1
	6	4	1	13	5	22.00	2	20	4	3	16	4
	4	6		—		23.00	3	12			2	3
	—			—		24.00		—			—	

The adaptability of the apparatus lies in the fact that by prolonging expulsion phase 1—the box being kept open and the lamp weak—even very damp samples can be treated; and if stronger lamps are used in phase 4 the drying can be made so effective that the humidity of the earth sample becomes fatal to the most xerophilous species so that they will leave the sample and fall down upon the collecting glass under the funnel.

My general impression of the course of drying and expulsion agrees in all essentials with that of Trägårdh & Forsslund (1932). When these authors speak of 'the sample being gradually desiccated from above downwards' this can be read immediately from the two humidity curves in Fig. 2. And when they further mention 'an actual flight in large numbers in the course of a comparatively short period of time' this corresponds to the large-scale emigration during phase 3 (cf. the curve in Thamdrup (1939), p. 61, in which about 20–10 % water content in raw humus (Maar) from heath soil corresponds to about 90–75 % R.H. in the same soil).

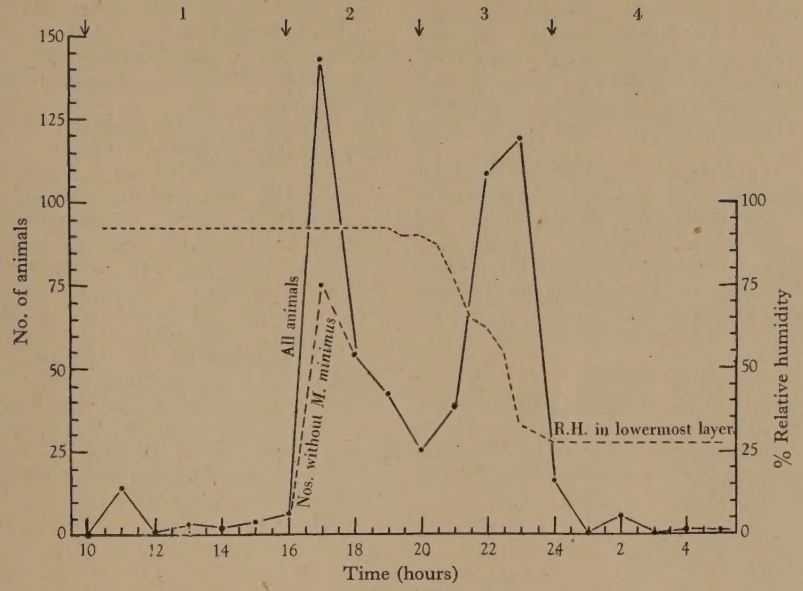

Fig. 5. 13 Oct. 1946. Apparatus 1. Numbers of Acarina and Collembola leaving the sample, with and without those of *Megalothorax minimus* (cf. Fig. 6).

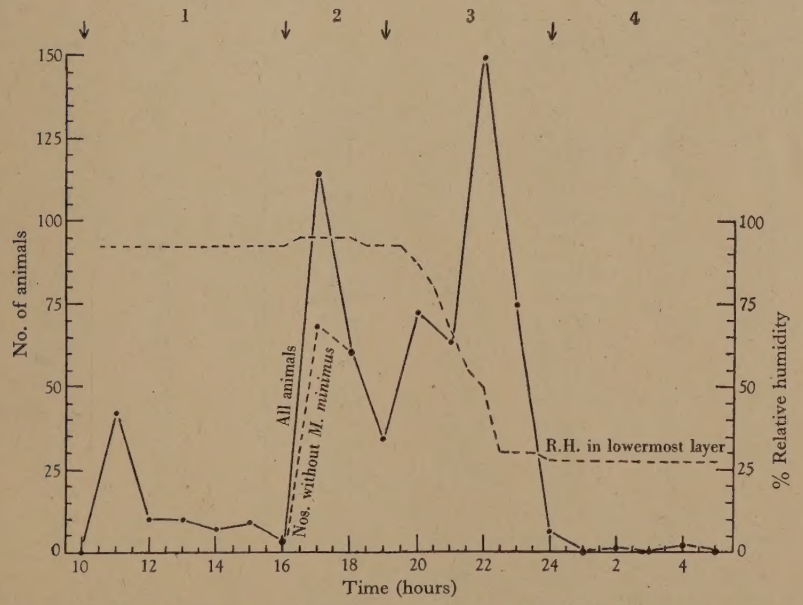

Fig. 6. 13 Oct. 1946. Apparatus 2. Numbers of Acarina and Collembola leaving the sample, with and without those of *Megalothorax minimus* (cf. Fig. 5).

Thamdrup also mentions that the R.H. in the raw humus from heath soil, even under a very hard drought (water about 30%), nowhere falls below about 90%. There is thus the possibility that about 90% R.H. is the optimal minimum threshold to the majority of the Collembola and Acarina living in the soil.

If possible I intend to continue these investigations, partly by means of thermo-electric measurements in the earth samples and humidity measurements in the mid-layer, partly with experiments on the resistance of the animals to temperature and humidity, with the purpose of better understanding the mode of action of the Tullgren apparatus, and the reliability of the figures which can be found by means of it.

SUMMARY

1. The model of the Tullgren apparatus used is seen in Fig. 1. The apparatus was employed both for qualitative and quantitative collecting of Collembola and Acarina in samples of a surface area of 0·001 sq.m. and a depth of 6–7 cm.

2. The results from using the apparatus are shown in Figs. 2–6 and Tables 1–6. The temperature was measured with mercury thermometers; the relative air humidity with Nielsen-Thamdrup sulphuric acid hygrometers.

3. The expulsion of the animals from the samples took place in four phases (Figs. 4–6).

4. 'Thin-skinned Acarina' are not less resistant to humidity than 'thick-skinned' ones (Table 1).

5. Sources of error are: (1) formation of dew on the inner side of the funnel—when the earth sample by mistake reaches right to the border of the netting and the temperature is too high in relation to the water-content of the sample, (2) paralysation when temperatures rise too high and too fast.

6. The apparatus can be used both for very moist localities—by prolonging phase 1—and for very dry ones—by prolonging and intensifying phase 4.

7. About 90% relative air humidity seems both in the samples and in the field to be the optimal minimum threshold for the majority of the Collembola and Acarina living in the soil.

APPENDIX

Table 2. *Data for Fig. 2*

	Temperature (° C.)		% R.H.			Temperature (° C.)		% R.H.	
Time	Inside sample	Outside sample	Lowermost layer	Surface	Time	Inside sample	Outside sample	Lowermost layer	Surface
09.45	19	20	—	90–85	19.30	35·5	40	90	—
10.00	21·5	23	—	85	20.00	36	40	90	—
10.30	22·5	23	95–90	75	20.30	37·5	40·5	90–85	—
11.00	23	23·5	95–90	75	21.00	38·5	40	80–75	—
11.30	23	24	95–90	75–70	21.30	40	40	65	—
12.00	23	24·5	95–90	—	22.00	41	40	65–60	—
12.30	23	25	95–90	65	22.30	41·5	39·5	55	—
13.00	23·5	25	95–90	65	23.00	42	39·5	35–30	—
13.30	23·5	25	95–90	65	23.30	41·5	39	30	—
14.00	23·5	25	95–90	65–60	24.00	42	39	30–25	—
14.30	23·5	25	95–90	65–60	00.30	42	39	30–25	—
15.00	23·5	25	95–90	—	01.00	41·5	38·5	30–25	15–10
15.30	23·5	25	95–90	60–55	01.30	41·5	38·5	30–25	—
16.00	23	25	95–90	60–55	02.00	41·5	38·5	30–25	15–10
16.30	31	37	95–90	55	03.00	41·5	38·5	30–25	—
17.00	33	39	95–90	30	04.00	41·5	38·5	30–25	—
17.30	33·5	40	95–90	30–25	05.00	41·5	38·5	30–25	—
18.00	33·5	40	95–90	—	13.30	42	39·5	30–25	—
18.30	34	40	95–90	30–25	16·00	43	40	30–25	—
19.00	34·5	40	95–90	—	16.30	43	40	30–25	15–10

Table 3. *Data for Fig.* 3

Time	Temperature (° C.) Inside sample	Outside sample	% R.H. Lowermost layer	Time	Temperature (° C.) Inside sample	Outside sample	% R.H. Lowermost layer
09.45	19	21	—	19.30	36	37·5	95–90
10.00	21	23·5	—	20.00	37	37·5	90–85
10.30	22	24·5	95–90	20.30	38	37·5	80
11.00	22·5	24·5	95–90	21.00	39	37·5	70–65
11.30	23	25·5	95–90	21.30	40	37·5	55
12.00	23	25·5	95–90	22.00	41	37·5	50
12.30	23	26	95–90	22.30	40·5	37	30
13.00	23	26	95–90	23.00	40·5	37	30
13.30	23	26	95–90	23.30	40·5	36·5	30
14.00	23	26·5	95–90	24.00	40	36·5	30–25
14.30	23	26	95–90	00.30	40	37	30–25
15.00	23	26·5	95–90	01.00	39·5	36	30–25
15.30	23	26	95–90	01.30	39·5	36	30–25
16.00	23	26·5	95–90	02.00	39·5	36	30–25
16.30	29	34·5	95	03.00	39·5	36	30–25
17.00	31·5	36·5	95	04.00	39·5	36	30–25
17.30	32·5	37	95	05.00	39·5	36·5	30–25
18.00	33	37	95	13.30	40	37	30–25
18.30	34	37·5	95–90	16.00	41	38	30–25
19.00	35	37	95–90	16.30	41	38	30–25

Table 4. *Data for Fig.* 4

Exp. no.	Hr.	...	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	Totals
1	Nos.	...	2	0	0	0	1	0	46	5	0	0	0	0	0	0	0	54
2	Nos.	...	2	0	0	0	2	1	68	1	0	0	0	0	0	0	0	74
3	Nos.	...	0	0	0	1	0	0	27	7	0	0	0	0	0	1	0	36
4	Nos.	...	0	1	0	0	0	1	9	2	0	0	0	0	0	0	0	13
5	Nos.	...	3	1	1	0	0	3	30	23	3	0	3	0	1	1	1	70

Table 5. *Data for Fig.* 5

Time ...	10.00	11.00	12.00	13.00	14.00	15.00	16.00	17.00	18.00	19.00	20.00	21.00	
Nos. ...	0	14	1	3	2	4	6	143 (75)	54	42	25	38	
Time ...	22.00	23.00	24.00	01.00	02.00	03.00	04.00	05.00	13.30	16.00	16.30		
Nos. ...	108	119	16	0	5	0	1	1	1	1	1	Total 585	

Table 6. *Data for Fig.* 6

Time ...	10.00	11.00	12.00	13.00	14.00	15.00	16.00	17.00	18.00	19.00	20.00	21.00
Nos. ...	0	42	10	10	7	9	3	114 (68)	60	34	72	63
Time ...	22.00	23.00	24.00	01.00	02.00	03.00	04.00	05.00	13.30	16.00	16.30	
Nos. ...	149	74	6	0	1	0	2	0	0	0	0	Total 656

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POLLEN COLLECTION BY HONEYBEES (*APIS MELLIFERA*)

By A. D. SYNGE, *Bee Department, Rothamsted Experimental Station, Harpenden, Herts.*

(With 9 Figures in the Text)

1. INTRODUCTION

Pollen traps have been used fairly extensively by various workers during the summer months to collect surplus pollen brought in by the bees. This pollen is used in the following spring to stimulate brood rearing at a time when pollen is in short supply. Todd & Bishop (1940) record the total weights of pollen brought in by colonies throughout the year in four localities in California. They state that the pollen cycles show similar trends in each locality for 2 years in succession, though neighbouring colonies may bring in very different actual quantities of pollen and work different crops. Only a very rough estimate of the constituent pollen species is given however. Eckert (1942) gives weekly total weights of pollen trapped from a succession of colonies for two seasons, this work also being carried out in California. Betts (1928, 1935) made a more systematic study of the plants worked for pollen in the neighbourhood of Camberley, by taking pollen loads from individual bees entering a hive; but, being more concerned with the total number of species worked and the proportion of mixed loads gathered, she gives no data on the relative amounts of the different pollens collected. Most other accounts of the sources of pollen supply and their importance to bees, such as those given in books on general beekeeping, are drawn from observations made of bees in the field and are, for this reason, biassed in favour of plants whose flowers grow at, or below, eye level and yield conspicuously coloured pollen. Throughout the seasons of 1945 and 1946 pollen has been trapped from colonies of honeybees (*Apis mellifera* L.) in the Home Apiary at Rothamsted and the daily catch analysed into its constituent pollen species in an endeavour to obtain a quantitative as well as a qualitative estimate of the pollen gathered by colonies of honeybees in this particular neighbourhood.

2. METHOD OF TRAPPING AND ANALYSIS OF POLLEN

(*a*) *Traps*

Trapping was begun in 1945 while the fruit trees were in flower, and various pollen traps were tested in order to find the type that would catch a satisfactory proportion of the pollen brought in by the bees. The trap in use was circulated between three hives, being in place on any particular hive one day in three. During the course of the season it became evident that the three colonies were obtaining their pollen to a large extent from different sources, with the result that correlations between weather conditions and the pollen species gathered were being masked. The results obtained in 1945 were only of use, therefore, in confirming the large-scale pollen trends found in 1946. In 1946 two identical traps were kept in continuous operation on two separate colonies, E 4 and K 5, from the first day in February, when pollen was seen being carried into the hives, until the end of the season.

The trap used in 1946 is shown in Fig. 1 and consists essentially of two strips of wire-gauze (5 meshes per in.) held vertically in a wooden framework with a 1½ in. space between them. Pollen loads scraped from bees' legs during their passage through the vertical screens fall through a horizontal wire-gauze screen into the collecting tray below. This tray, being wider than the distance between the screens, forms an alighting board for the bees. It could with advantage be wider still, since large loads that do not drop through the gauze into the tray immediately are sometimes pushed off on to the ground when large numbers of bees are leaving the hive. The horizontal gauze screen should be fixed to the upper part of the trap, and the tray so arranged that it can be drawn out sideways leaving a false front, and the trap itself can be emptied at any time of the day without presenting a different appearance to the returning bees. To ensure uniform results these alterations were not made during the 1946 season.

The efficiency of the trap was tested in two different ways. The percentage of loads caught was determined in the first method by counting 100 bees entering the hive with pollen on their legs, after the trap had been emptied, and finding the number of loads left in the tray.

To ensure that no pollen-carrying bees were missed, the counts were made at a time of year when all the pollen was light coloured and on days when there were not too many bees flying for accurate counting to be possible. Eight such counts were made, giving an average of $25{\cdot}3\,\% \pm 0{\cdot}78$ for the amounts of pollen caught by the trap. The second method was only used once. All combs containing

larvae, eggs or stored pollen were removed from a colony, replaced by empty combs and a trap fixed on to the hive. After 4 days the colony was examined and 10·35 g. of pollen removed from the combs, 6·20 g. of pollen having been caught in the trap over the same period, so that 37·5 % of the pollen brought into the hive was apparently trapped. However, as some very young larvae were found in the hive at the end of the period, probably some of the pollen was utilized by the bees before it could be weighed.

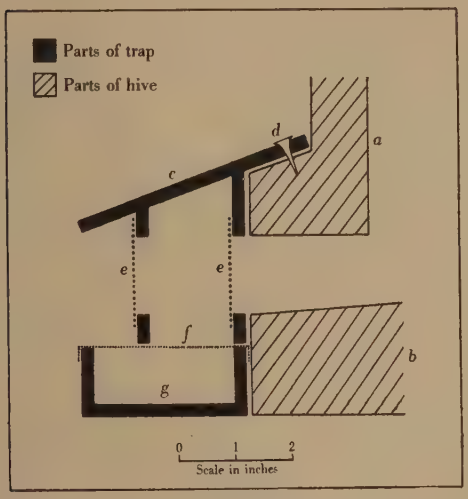

Fig. 1. Cross-section of pollen trap in position on National hive. *a*, brood chamber; *b*, floor board; *c*, roof of trap; *d*, screw; *e*, 5 meshes per in. wire-gauze screens; *f*, fine wire-gauze screen; *g*, collecting tray.

The first method is, therefore, taken as giving the more accurate result. An efficiency of 25 %, although low if the object of trapping is the collection of pollen in bulk, was found suitable for the purpose of detailed daily examination. A trap of higher efficiency, by interfering drastically with the normal economy of the colony, would have made it impossible, unless special precautions were taken, to trap pollen from the same colonies throughout the whole season.

Neither of these methods can give exact results, since the percentage of loads trapped depends on the size of the loads, which vary considerably. There is a difference in the average size of loads collected from different plants, for example *Brassica* and *Papaver* loads are conspicuously large whereas those of *Lotus* are very small. In 1945 a hundred loads of each of the pollens noted in Table 1 were taken at random and measured with callipers in order to determine the number of large loads present.

Pollen loads from *Brassica* (*alba*) and *Hedera helix* collected in September and October 1946 were also examined to find the percentage retained by a sieve of perforated zinc with holes 2 mm. in diameter. (Table 2).

Table 1. *Size of pollen loads*, 1945

Plant	No. of loads in 100 with diameter greater than 3·5 mm.
Sinapis (*sinapistrum*)	59
Papaver rhoeas	42
Brassica (*alba*)	36
Vicia faba	16
Red clover	16
Hedera helix	15
Epilobium angustifolium	13
White clover	11
Onobrychis sativa	5
Lotus corniculatus	0

The percentage of pollen caught by the trap is also affected by changeable weather conditions which cause bees to return to the hive before a full load has been collected.

The two colonies used for trapping in 1946 were at the beginning of the season of approximately equal strength, covering eight standard brood combs. The average tongue, wing and leg lengths of bees collected from these two colonies in November 1945 showed no significant differences. Neither colony produced any surplus honey, both colonies were given syrup during April when they were almost entirely without stores and both were fed on a certain amount of pollen throughout the season which they took readily. Neither stock swarmed. The poor performance of these two colonies cannot be attributed to the pollen traps since other colonies in the apiary, though working normally, were equally short of stores at the end of the season. The weight

Table 2. *Size of pollen loads*, 1946

Plant	No. of loads examined	No. of loads of width greater than 2·0 mm.	Percentage of loads of width greater than 2·0 mm.
Brassica (*alba*)	780	710	81
Hedera helix	860	390	45

of pollen trapped during 1946 was 1480 g. from colony E4, and 1389 g. from colony K5, which, taking the efficiency of the traps as 25%, means that the two colonies collected 5920 and 5556 g. respectively during 1946. The corresponding figures given by Todd & Bishop (1940) ranged from 8077 g. in the Sierra Nevadas to 17,984 g. in the Sacramento Valley.

(*b*) *Analysis of pollen*

The traps were emptied every evening and the contents weighed the following morning. On days when the catch was heavy, only a proportion, never less than one-fifth by weight, was taken for further examination and the final counts multiplied accordingly. The pollen was then sorted by eye according to colour and texture, size and shape of load being useful indications, and a representative sample of each type of pollen mounted and examined under the microscope. The pollen was stained with basic fuchsin and mounted in glycerin jelly for comparison with a collection of type slides prepared in this way. In most cases the identification was confirmed by finding bees at work on the plant in question with pollen of the correct colour on their legs. In the case of pollens containing anthocyanins, the characteristic colours obtained on addition of acid and alkali were found useful for identification, particularly for distinguishing *Papaver rhoeas* from *P. orientale*. When the preliminary sorting had been checked by microscopical examination, the numbers of loads of each pollen were counted. All figures given in this paper are for the number of loads trapped, not the total number of loads collected by the colony. The pollens concerned have usually been identified to the genus and in some cases to the species. When the genus or species is assumed from knowledge of the local flora rather than a clear-cut distinction in the pollen grain, the name is given in brackets.

In some families such detailed identification was not attempted. In the Compositae, members of the tribe Cynareae have been identified to the genus, all the Cichorieae have been grouped together, *Dahlia* has been distinguished as a separate genus and all other Compositae have been classed together as *Aster* type. Pollens of the Gramineae and Umbelliferae, both families with a characteristic pollen type subject to only minor modifications among the genera and of no great importance as pollen producers, have not been identified beyond the family. The name 'red clover' is used to cover *Trifolium pratense* and *T. incarnatum*, though the majority of the pollen is almost certainly the former, similarly, 'white clover' covers *T. repens* and *T. hybridum*. The labour involved in mounting the large number of loads of these two pairs of species in order to discriminate between them in the absence of a colour distinction was not thought worth undertaking. (Some confusion in the sorting by eye of red clover loads was caused by the large numbers of black fungus spores sometimes present.) Likewise, owing to the rather indistinct colour division between *Prunus* and *Pyrus*, only a rough estimate is given of the division of the total amount of fruit blossom pollen between the two genera. I am indebted to Dr R. Melville for the identification of one of the pollens as probably being *Filipendula ulmaria*.

3. RESULTS OF ANALYSIS

Table 3 gives a list of the total number of pollen loads of the different plant species trapped from the two colonies in 1946 together with the corresponding 1945 percentages which have been adjusted to allow for the early spring pollen, assuming that it formed the same proportion of the year's catch as in 1946. It is apparent that the bulk of the pollen came from comparatively few plants and that the clovers formed the most important source, yielding almost 50% of the total. There is obvious agreement in outline between the 2 years, though, owing to the different method of trapping employed in 1945, no detailed comparison of the number of the pollen loads collected can be made. There are, however, a few outstanding differences in the relative importance of some species, which can be attributed to the weather conditions prevailing during the flowering periods of the plants concerned in 1945 and 1946.

The weather was bad during early June in 1946 and in addition the late season appeared to affect *Onobrychis* more than white clover, causing the two plants to come into competition, which was not the case in 1945. As a result the bees virtually missed the first crop of *Onobrychis* in 1946. In the same way, *Crataegus* was of more importance in 1945 when a very fine spell of weather occurred during the flowering season and a large amount of pollen was collected in a few days. In 1946 the flowering period was considerably prolonged, but at no time was the weather really favourable and comparatively little pollen was collected.

It can be seen from Figs. 2 and 3* that the main pollen flow from any plant occurs when a rise in temperature follows a cold period, though the flow does not necessarily continue at the same intensity until the temperature drops, often failing while the temperature still rises. This relation between pollen gathering and temperature is probably due as much to the increase in flowering as to the greater activity of the bees, both being caused by a rise in tempera-

* The original data for these and some other figures for which no tables are given here, are being deposited for reference at Rothamsted Experimental Station.

Table 3. *Pollen loads trapped in* 1945 *and* 1946

% of total	Colony E4, 1946 Species	No. of loads	Colony K5, 1946 Species	No. of loads	1945* Species
33	White clover	67,444	—	—	—
23	—	—	Red clover	45,148	—
22	—	—	—	—	Red clover
17	—	—	White clover	32,415	*Onobrychis sativa*
14	Red clover	29,386	—	—	—
13	Fruit (*Prunus* 4,000, *Pyrus* 22,100 approx.)	26,129	—	—	—
10	—	—	Fruit (*Prunus* 3,800, *Pyrus* 16,000 approx.)	19,771	—
9	—	—	—	—	White clover
9	—	—	—	—	*Crataegus*
8	*Onobrychis sativa*	15,784	*Onobrychis sativa*	14,669	—
7	—	—	—	—	*Brassica + Sinapis*
6	*Brassica + Sinapis*	12,029	—	—	—
5	—	—	*Brassica + Sinapis*	9,623	—
4	—	—	—	—	*Hedera helix*
3	*Populus*	5,926	Cichorieae	5,601	—
3	—	—	*Populus*	5,370	—
2	*Vicia faba*	4,979	*Fraxinus excelsior*	4,685	*Papaver rhoeas*
2	*Ranunculus*	4,967	*Rubus fruticosus*	4,480	*Rubus fruticosus*
2	Cichorieae	4,016	*Crataegus*	4,379	—
2	*Crataegus*	3,414	*Epilobium angustifolium*	3,576	—
2	—	—	*Salix*	3,160	—
2	—	—	*Acer*	2,933	—
1	*Fraxinus excelsior*	3,068	*Hedera helix*	2,610	*Epilobium angustifolium*
1	*Acer*	3,018	*Betula*	2,328	Cichorieae
1	*Rubus fruticosus*	3,016	*Bryonia dioica*	2,038	—
1	*Ulex europaeus*	2,956	*Rosa*	2,008	—
1	*Quercus*	2,587	*Filipendula ulmaria*?	1,942	—
1	*Ulmus*	1,978	*Berberis*	1,653	—
1	*Papaver rhoeas*	1,834	*Aster* type	1,626	—
1	*Epilobium angustifolium*	1,735	*Ranunculus*	1,507	—
1	*Bryonia dioica*	1,573	*Castanea sativa*	1,456	—
1	*Aesculus hippocastanum*	1,232	*Allium*?	1,387	—
1	*Castanea sativa*	1,107	*Ulmus*	1,370	—
1	—	—	*Aubrietia*	1,069	—
<1	Thistles	639	*Dahlia*	860	*Aster* type
<1	*Rosa*	608	*Buxus sempervirens*	809	*Bryonia dioica*
<1	*Aubrietia*	483	*Ulex europaeus*	701	*Ranunculus*
<1	*Berberis*	424	*Veronica*	675	*Allium*?
<1	*Salix*	392	*Cupressus* or *Taxus*	611	*Vicia faba*
<1	*Viola tricolor*	253	*Papaver orientale*	561	*Lotus corniculatus*
<1	*Allium*?	228	*Aesculus hippocastanum*	521	*Acer*
<1	*Aster* type	195	Umbelliferae	510	*Aesculus hippocastanum*
<1	*Papaver orientale*	154	Thistles	287	*Rosa*
<1	Shirley poppy	137	*Anemone*	268	*Convolvulus arvensis*
<1	*Lotus corniculatus*	124	*Viola tricolor*	238	*Buddleia*
<1	*Buxus sempervirens*	114	*Vicia faba*	223	Umbelliferae
<1	*Veronica*	114	*Plantago*	214	*Cerastium*
<1	*Scilla*	103	Gramineae	184	Thistles
<1	—	—	Shirley poppy	127	*Tropaeolum*
<1	—	—	*Fragaria*	125	*Viola tricolor*
<1	—	—	*Scilla*	121	—
<1	—	—	*Rumex*	119	—
	Unidentified (about 30 species) and mixed loads	710	Unidentified (about 30 species) and mixed loads	670	
	Total	203,590	Total	193,240	

(Pollens of which less than 100 loads were trapped are shown in Table 4.)

* Pollen collected before trapping was begun is taken as 22 % of year's total.

ture. On the other hand, a prolonged spell of bad weather covering the whole of the possible flowering period of a plant, will probably depress flowering as well as bee activity and result in the collection of little or no pollen from a plant which may potentially be a heavy pollen yielder.

Table 4 gives the seasonal distribution of the pollen sources, classified according to their relative importance. The pollen-gathering season can be divided roughly into four main periods which have held good in this locality in two successive years, corresponding periods being 2–3 weeks later in 1946

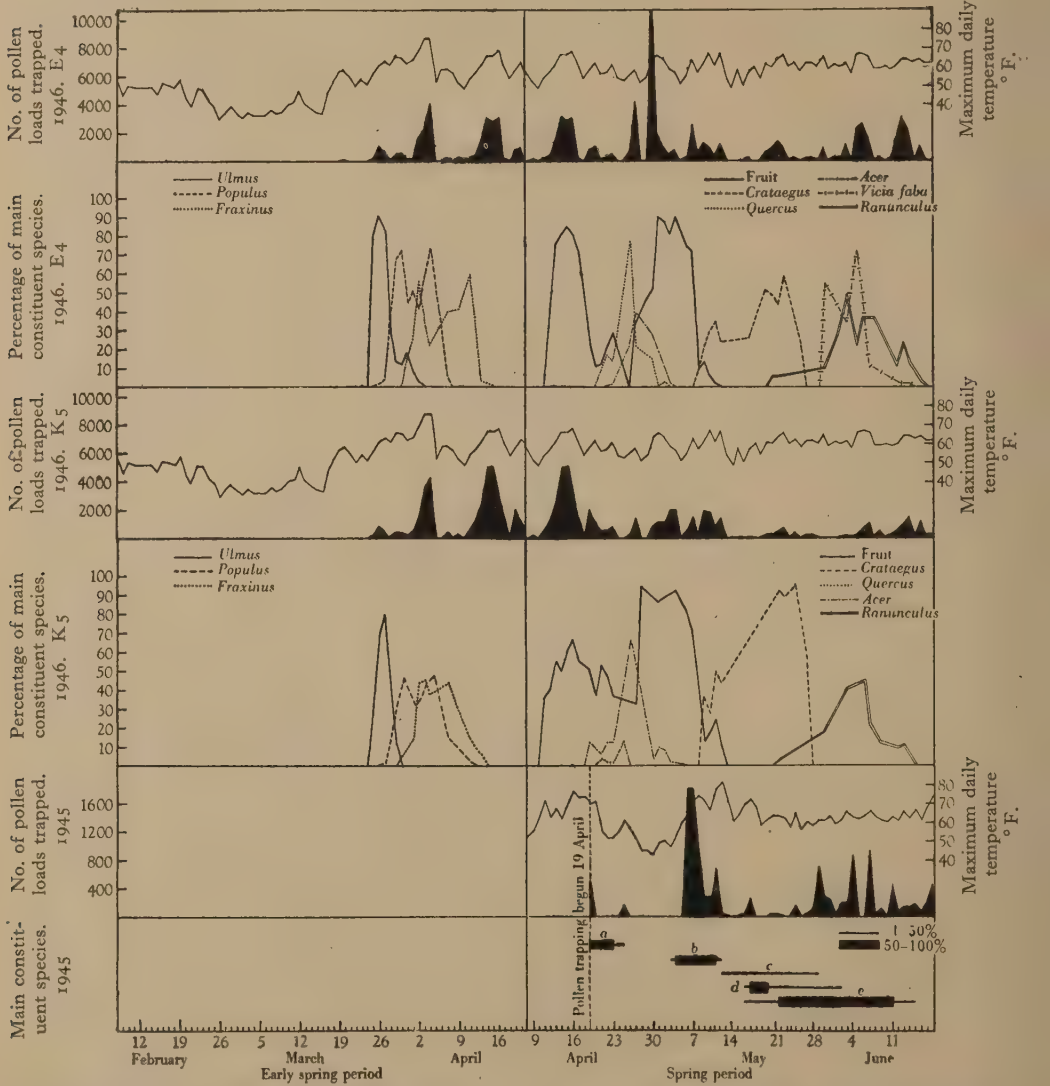

Fig. 2. Total daily numbers of pollen loads trapped in 1945 and 1946 with maximum daily temperatures and percentages of main constituent pollen species for days on which the total number of loads exceeded 100. *a*, fruit; *b*, *Crataegus*; *c*, *Vicia faba*; *d*, *Trifolium incarnatum*; *e*, *Onobrychis sativa*.

than 1945. The early spring pollen comes mainly from the forest trees which characteristically yield a large amount of pollen in a very few days (Fig. 2). The double peak in the percentage of *Populus* pollen is due to the different flowering time of the three species locally common, *Populus nigra* var. *italica* flowering earlier than *P. nigra* and *P. canadensis*. The main spring pollen flow comes from the rosaceous trees and shrubs (Fig. 2). *Prunus spinosa*, *P. avium* and cultivated varieties of cherry, plum and pear form the first peak in the percentage of fruit pollen and cultivated varieties of apple the second, followed

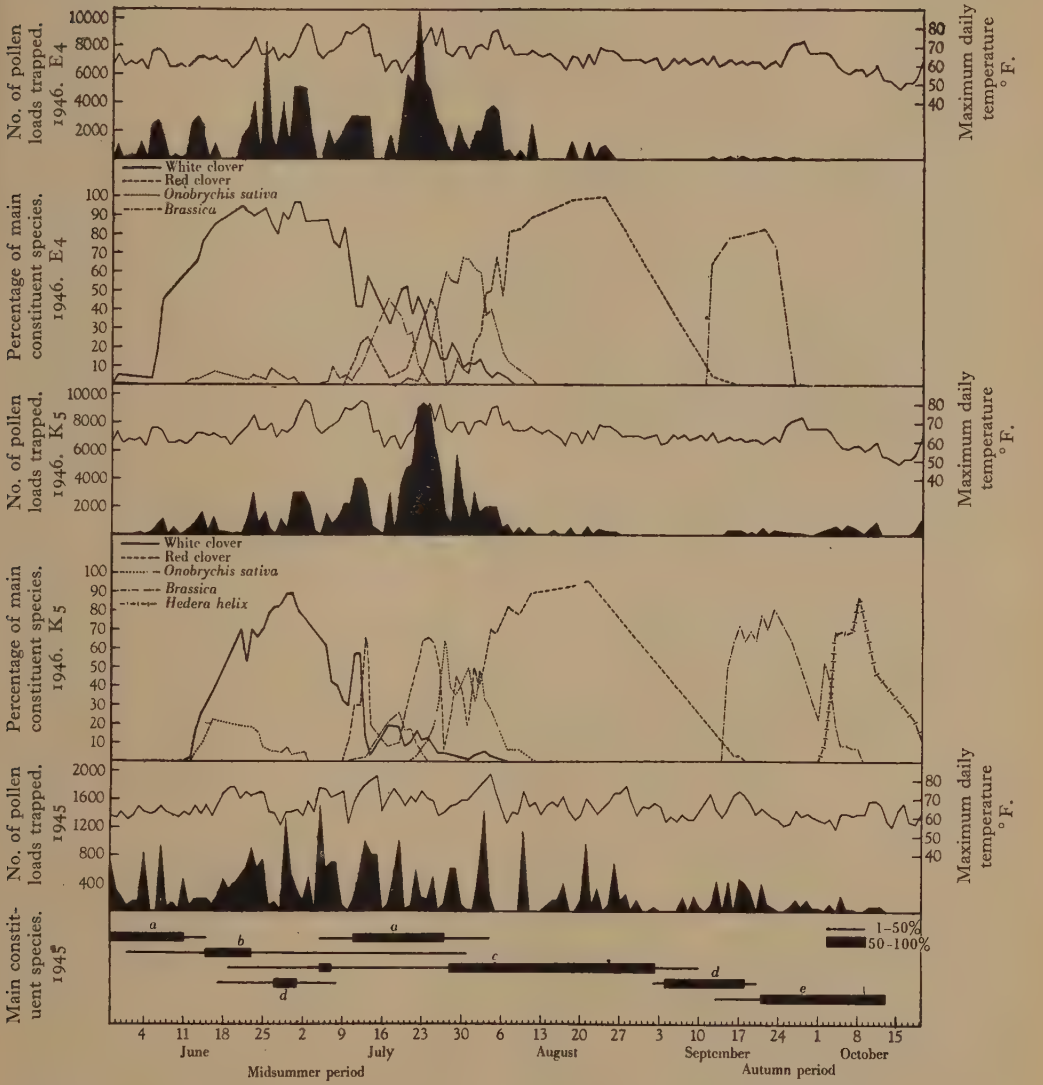
No. of pollen loads trapped. 1946. E4
Maximum daily temperature ° F.
White clover
Red clover
Onobrychis sativa
Brassica
Percentage of main constituent species. 1946. E4
No. of pollen loads trapped. 1946. K5
Maximum daily temperature ° F.
White clover
Red clover
Onobrychis sativa
Brassica
Hedera helix
Percentage of main constituent species. 1946. K5
No. of pollen loads trapped. 1945
Maximum daily temperature ° F.
Main constituent species. 1945
1–50%
50–100%
4 11 18 25 2 9 16 23 30 6 13 20 27 3 10 17 24 1 8 15
June July August September October
Midsummer period
Autumn period

Fig. 3. Total daily numbers of pollen loads trapped in 1945 and 1946 with maximum daily temperatures and percentages of main constituent pollen species for days on which the total number of loads exceeded 100. *a*, *Onobrychis sativa*; *b*, white clover; *c*, red clover; *d*, *Brassica*; *e*, *Hedera helix*.

Table 4. *Seasonal distribution of pollen sources and their relative importance in 1945 and 1946**

	1 February–14 April	8 April–31 May	12 May–10 September	1 September–31 October
Main pollen sources	*Fraxinus* (*excelsior*) *Populus* *Ulmus* (*glabra*)	*Crataegus* *Prunus* *Pyrus*	*Onobrychis sativa* Red clover *Sinapis* (*sinapistrum*) White clover	*Brassica* (*alba*) *Hedera helix*
Important pollen sources	*Buxus sempervirens* *Cupressus* or *Taxus* *Salix*	*Acer* *Aesculus hippocastanum* *Aubrietia* *Berberis* *Betula* *Brassica* (*oleracea*) Cichorieae *Quercus* *Salix* *Ulex europaeus*	*Bryonia dioica* *Castanea sativa* Cynareae *Epilobium angustifolium* *Filipendula ulmaria*? *Papaver rhoeas* *Ranunculus* *Rosa* *Rubus fruticosus* *Vicia faba*	*Aster* type (*Aster* and *Helianthus*) Cichorieae *Dahlia* *Rosa* *Veronica*
Unimportant pollen sources	*Anemone* *Aster* type (*Doronicum*) *Chionodoxa* Cichorieae *Corylus* *Crocus* *Erica* *Forsythia* *Lamium purpureum* *Mercurialis perennis* *Tulipa* *Ulex europaeus*	*Fragaria* *Lamium purpureum* *Oxalis* *Ranunculus* *Rubus idaeus* *Scilla* *Syringa* *Tulipa* Umbelliferae *Veronica*	*Althaea* *Anchusa* *Armeria* *Aster* type *Buddleia* *Calystegia sepium* *Campanula* *Centauria cyanus* *Centauria nigra* *Cerastium* *Cistus* *Clarkia elegans* *Convolvulus arvensis* *Cornus* *Cucurbita pepo* *Epilobium* (*hirsutum*) *Eschscholtzia* *Geranium* Gramineae *Hydrangea* *Ilex* *Knautia* *Ligustrum* *Linum* *Lonicera* *Lotus corniculatus* *Lupinus* *Lythrum salicaria* *Malva* *Melilotus* *Papaver orientale* *Papaver* (Shirley poppy) *Pinus* *Plantago* *Polemonium* *Poterium* *Rumex* *Salvia* *Symphoricarpus* *Symphytum* *Tilia* Umbelliferae *Veronica* *Viola tricolor*	*Anemone japonica* *Bryonia dioica* *Centaurea cyanus* *Epilobium angustifolium* *Gladiolus* *Papaver* (Shirley poppy) *Tropaeolum*

* The variability of different years makes it difficult to give exact dates for the seasons. The dates for the main pollen sources can be derived from Figs. 2 and 3.

later by *Crataegus*. These plants provide a rather more sustained supply of pollen than the forest trees. The midsummer period covers the time of the main nectar flow and the principal pollen yielding plants are legumes (Fig. 3). Although the greatest weight of pollen trapped on a single day came from the fruit blossom, the legumes, owing to their prolonged season of flowering (11 weeks for white clover), provide a very large proportion of the total pollen collected during the year. Pollen was collected from both first and second crops of *Onobrychis*, but from the second crop only of red clover. Red clover is grown round Harpenden for seed on a fairly large scale and the second or seed crop fills the August gap to a certain extent, but there is a paucity of lesser pollen plants at this time. *Tilia* is one of the main nectar sources in this neighbourhood, but only two loads of *Tilia* pollen were trapped in the two seasons. It is of interest to note that a bumble-bee colony kept in the same apiary in 1945 was known to be collecting *Tilia* pollen. The autumn period (Fig. 3) is characterized by a large number of moderately important pollen plants the chief being *Brassica* (*alba*), grown on a field scale for green manure and *Hedera helix*.

The Home Apiary is situated on the edge of Rothamsted Experimental Farm. There are thus on the west side permanent pastures, arable fields and mixed leys, including crops of field beans, red and white clovers and *Onobrychis sativa* and on the east side residential houses with fairly large gardens. Features of the immediate neighbourhood of the apiary are a lime (*Tilia*) avenue, a small orchard and a group of allotments. There are a certain number of hedgerow trees, but no true woodland and on the east side there is a gorse-covered common.

If Table 3 is examined with regard to the local flora, it is apparent that the herbaceous garden plants, which are probably as abundant in this neighbourhood as any, were of little use to the bees for pollen with the exception of *Aubrietia*, *Dahlia*, *Helianthus* and *Aster*. Weeds, including *Taraxacum*, *Crepis*, *Carduus*, *Veronica* and *Papaver rhoeas* yielded more pollen, possibly due to the proximity of the allotments. But the great majority of the pollen came from plants growing on a field scale, trees and to a lesser extent shrubs. The importance of leguminous crops and fruit trees as producers of pollen has long been recognized, but the value of the forest trees, accentuated as it is by their early flowering, has been underestimated.

Table 5 shows the relative importance of these three groups of plants to the two colonies examined, which had access to a moderate number of trees only, so that it seems reasonable to suppose that colonies within flight range of woods have a supply of early pollen limited only by weather conditions and the short flowering periods of the trees concerned.

Table 5. *Percentage of pollen loads trapped in 1946 from main plant types*

	Colony E4	Colony K5
Leguminous plants	57	48
Rosaceous trees and shrubs	16	15
Forest trees	9	12
Other plants	18	25

4. AVAILABILITY OF POLLEN

Parker (1926), by counting the number of pollen-gathering bees working any particular crop at intervals during the day, showed that different plant species have definite times of the day at which their pollen is available. Details are given for three species, *Trifolium repens*, *Melilotus alba* and *Rosa setigera*, and although the figures are rather small and appear to refer only to a single day, they show that while *Trifolium repens* and *Melilotus alba* yield pollen from late morning to afternoon, *Rosa setigera* yields pollen only in the early morning.

On 12 days during the midsummer pollen period in 1946 the trap on one of the hives, E4 or K5, was emptied at hourly intervals and each hour's catch analysed separately. Observations were made concurrently on the pollen-yielding flowers of that period, but unfortunately it was not always possible to carry out both sets of observations on the same days.

(*a*) *Relation between pollen collecting by bees and floral mechanism for the release of pollen*

Pollen is made available to bees through the opening of the flower and through the dehiscence of the anthers; whichever of these two operations occurs last is naturally the limiting factor for the bee and there is no uniformity among plants in the order of these happenings. Of the seven types of flowers examined in detail: in four, red and white clover, *Vicia faba* and *Papaver rhoeas*, the anthers dehisce in the closed bud; in two, *Epilobium angustifolium* and *Ranunculus*, the flowers open with the anthers intact; and in one, *Brassica alba*, the two operations occur at almost the same time. These facts, together with the differences in size and structure, necessitated the use of slightly different techniques for the examination of each flower, but the general method was to discover first whether flower opening or anther dehiscence was the limiting factor in the release of pollen and then to make hourly counts of the relevant factor on a group of flowers. Table 6 gives all the data obtained in this way in 1946.

(1) In the case of *Vicia faba*, an important pollen plant for colony E4 in early June, a row of

Table 6. *Summary of data on pollen availability*

Species	Type of individual counted	No. of counts	Dates	No. on which count was made	Totals for hourly intervals (G.M.T.) for all days on which counts were made									
					Morning					Afternoon				
					7–8	8–9	9–10	10–11	11–12	12–1	1–2	2–3	3–4	4–5
Trifolium pratense	Flowers	3	21, 23, 26 Aug.	20 inflorescences	—	51	145	187	198	181	127	152	100	71
T. repens	Flowers	6	14, 18, 20, 21, 25, 27 June	Average of 16 inflorescences	—	71	130	108	77	95	61	24	14	5
Vicia faba	Flowers	3	13, 14, 15 June	16 plants	0	7	54	54	47	108	121	102	68	8
Ranunculus acris	Anthers	2	12, 13 June	Average of 15 flowers	6	93	143	74	25	38	34	16	3	2
Papaver rhoeas	Flowers	7	23–29 July	Bed of plants	90	0	0	0	0	0	0	0	0	0
Epilobium angustifolium	Anthers	2	23, 24 July	10 inflorescences	192	63	62	40	16	14	52	33	35	24
Brassica alba	Flowers	4	1–4 Aug.	10 inflorescences	166	3	2	1	2	1	1	0	0	0
Brassica alba	Bees	3	26, 29, 31 July	Total no. of bees at each count	38	51	44	48	52	44	44	31	9	—
				No. of bees with pollen	30	38	26	23	11	3	2	0	0	—
				Percentage of bees with pollen of total	79	75	59	48	21	7	5	0	0	—

16 plants was examined at hourly intervals and the standard of each flower that had opened in the preceding hour painted, a different colour being used on each day. In addition an individual record was kept of each of the 39 flowers opening during 4 days on three particular plants. It was found that each flower opened on three successive days, closing on the first two nights. The mean times (G.M.T.) of opening for the 39 flowers watched individually were, on the first day $13{\cdot}5 \pm 0{\cdot}024$, on the second day $12{\cdot}5 \pm 0{\cdot}022$ and on the third day $9{\cdot}9 \pm 0{\cdot}048$. The same differences are shown in Fig. 4, which gives the age of flowers

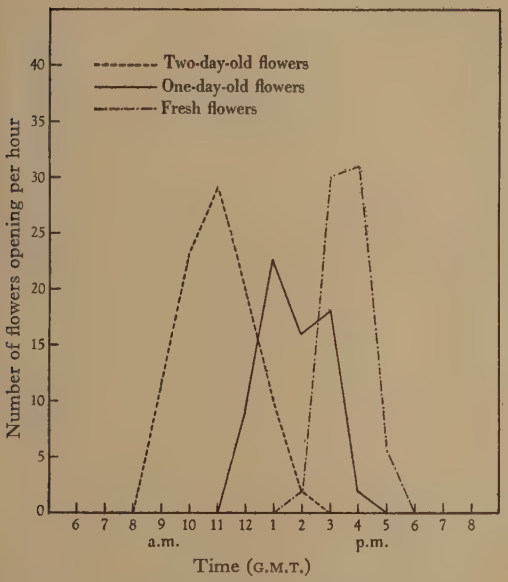

Fig. 4. Time of opening of *Vicia faba* flowers of different ages on 15 June 1946.

opening throughout 1 day on the whole row of plants. It is reasonable, therefore, to assume that most *V. faba* pollen is available in the late afternoon when young flowers are first opening, and hourly trapping (Fig. 5) showed that this pollen is indeed brought into the hive late in the day, though unfortunately figures were only obtained for days towards the end of the *V. faba* pollen flow. A small point of interest in the behaviour of bumble-bees visiting *V. faba* for nectar was noticed while watching the flowers. These bees were seen to bite holes at the base of unopened flowers and insert their proboscis, so that the flower evidently secretes nectar before it opens. The late opening of the flowers may therefore be the cause of this well-known abnormality in the behaviour of bumble-bees.

(2) The other main source of pollen in early June was *Ranunculus*. Sleep movements of these flowers occurred so early or late in the day that they did not affect the visiting bees and the limiting factor in the release of pollen was anther dehiscence.

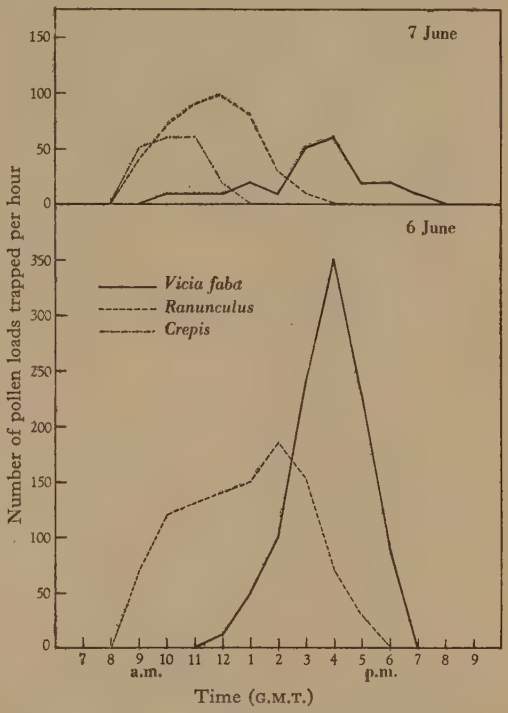

Fig. 5. Number of pollen loads of *Vicia faba, Ranunculus* and *Crepis* trapped at hourly intervals from colony E4 on 2 days in 1946.

The technique adopted in this case was the hourly removal of dehisced anthers from a number of marked flowers. Examination of intact flowers at the end of the day showed that this removal had at any rate no large effect on the total number of anthers of a treated flower dehiscing in the day. A definite morning peak of anther dehiscence can be seen from Table 6, and Fig. 5 shows that *Ranunculus* pollen collection was correspondingly early compared with that of *Vicia faba*.

(3) In the case of both red and white clovers, where the anthers dehisce in the bud, sleep movements of the flowers were the limiting factor to bees seeking nectar and pollen. The painting technique

used with *V. faba* was only employed on 1 day on 20 inflorescences of white clover, but it showed that the first flowers to open in the morning were those that had been open the previous day (Table 7).

All other observations on both the clovers were made by removing freshly opened flowers at hourly intervals, the age of the flowers not being taken into consideration. The results given in Table 6 show that flowers opened fairly continuously throughout the day, white clover tending to be slightly earlier than red. In the same way pollen collecting was usually maintained at a fairly steady level from 10.0 a.m. to 4.0 p.m. (G.M.T.), white clover usually reaching a maximum from 12.0 to 1.0 p.m. (Table 8 white clover and Fig. 6 red clover).

The number of bees counted bears a direct relationship to the amount of pollen available only if the total population increases and decreases with the pollen supply. If, however, the population is constant throughout the day, an increase in the pollen supply shortens the time taken to collect a full load, but does not affect the length of time spent flying to and from the hive. This results in a smaller proportion of the population being present in the clover field at any one time and a correspondingly lower count.

It is not known whether the population working a crop of red clover in full flower is constant, nor has it been proved that a bee will gather a load faster when more pollen is available, though it seems a

Table 7. *Numbers of white clover flowers opening on twenty inflorescences*, 18 *June* 1946

	Morning				Afternoon		
Time (G.M.T.) ...	8–9	9–10	10–11	11–12	12–1	1–2	2–3
Fresh flowers	2	12	30	18	26	9	1
Day-old flowers	15	22	3	1	1	0	0
Totals	17	34	33	19	27	9	1

Table 8. *Number of loads of white clover pollen collected by colony E* 4 1946

	Morning				Afternoon				
Time (G.M.T.) ...	8–9	9–10	10–11	11–12	12–1	1–2	2–3	3–4	4–5
7 June	3	8	107	105	209	108	100	27	0
13 June	0	5	680	160	410	250	280	159	8
14 June	2	67	177	195	443	191	222	316	75
21 June	0	54	225	288	460	177	170	115	12
25 June	0	162	327	375	812	625	454	429	83
Totals	5	296	1516	1123	2334	1351	1226	1046	178

Minor peaks in both flower opening and pollen collecting of white clover were found on some of the days, but these were probably not significant and could not be correlated with each other when both sets of data referred to the same day. Butler (1941) states that the honeybee exhibits two peak periods of activity when working red clover for pollen, one about 10.30 a.m. and the other about 3.0 p.m. (G.M.T.). He suggests that the plants reach their peak of pollen dehiscence at these times.

No evidence for these two peaks in either pollen collection or flower opening was found in this work, the dip in Fig. 6 being quite definitely due to cloud. The two results are not necessarily conflicting, however, since the technique employed was different in the two cases. Butler's estimates, apart from 1 day when bees were collected hourly from the alighting board of a hive, are based on 10-min. counts, made at hourly intervals, of the number of pollen-gathering bees seen working part of a red clover field.

reasonable assumption. But if these two conditions are assumed, then the increased number of open flowers and the greater number of red clover loads brought back to the hive at midday, as found in this work, would accompany a decrease in the number of pollen-collecting bees present in the field at one time as found by Butler.

(4) The pollen-releasing mechanism was essentially the same in *Papaver rhoeas* as in the clovers and depended on the opening of the flower, the anthers having dehisced overnight. The same technique, hourly removal of open flowers, could therefore be used, but in actual fact no flowers were ever found to open later than 8.0 a.m. (G.M.T.) when the first observations of the day were made. *Papaver* pollen was always the earliest to be collected by the bees and very little was ever brought in during the afternoon. Fig. 6 shows pollen collection on 2 days during the red clover pollen flow. The plants used for these experiments were mainly Shirley poppies mixed

with a few wild *P. rhoeas* plants. The bees worked the flowers for pollen only.

(5) The pollen-releasing mechanism of *Epilobium angustifolium* was essentially the same as that of *Ranunculus* and the same technique, removal of anthers, was employed. After reaching a maximum early in the morning, a steady rate of low anther dehiscence was found throughout the rest of the day (Table 6), and pollen collection, though on a small scale, followed the same trend.

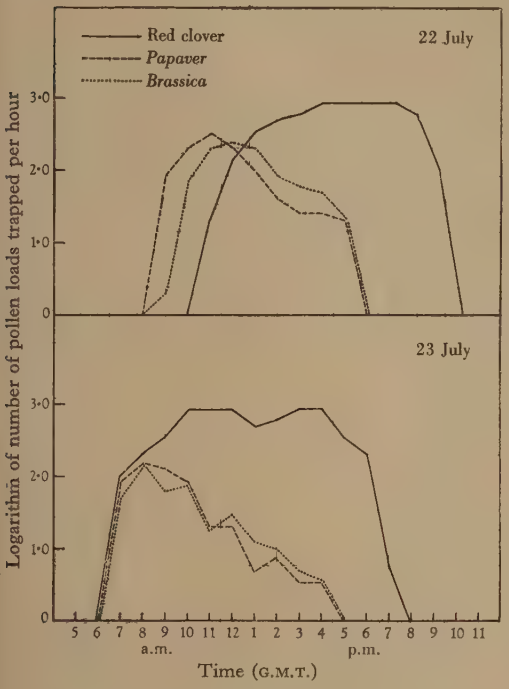

Fig. 6. Logarithm of number of pollen loads of red clover, *Papaver* and *Brassica* trapped at hourly intervals from colony K5 on 2 days in 1946.

(6) In *Brassica alba* all the anthers of a flower were found to dehisce very shortly after the flower had opened, so for ease of examination flower opening was taken as the limiting factor and was found to occur almost entirely before 8.0 a.m. (G.M.T.). Pollen collection (Fig. 6) was also restricted mainly to the morning. In addition, hourly counts were made on plots of *B. alba* of the number of bees present with and without pollen, and Table 6 shows that the number of pollen gatherers drops off steadily through the day in agreement with the data obtained from the pollen trap. Bees working these flowers at all times of the day were seeking nectar and may, as a result of being covered from the freshly dehisced anthers, have collected pollen only incidentally. Bees have, however, been observed working giant sunflowers for nectar and, though covered with pollen, they made no attempt to pack it into their pollen baskets and sometimes even cleared it off their bodies. From this it appears that bees are not compelled to collect pollen, even though they come in contact with it while seeking nectar.

(7) Evidence was obtained on the time of day when pollen was collected from two other plants, *Crepis* and *Rubus fruticosus*, the former apparently yielding pollen in the morning (Fig. 5) and the latter in the afternoon, but no detailed study of the flowers was attempted. A few observations on *Crepis taraxacifolia* showed that a certain number of the disk florets opened early every day, the styles of which, all expanding simultaneously, expelled pollen during the course of the morning, the process usually being complete by midday, after which the ray florets closed. The limiting factor to the bees was in this case therefore neither flower opening nor anther dehiscence, but the rate of growth of style.

(*b*) *Relation between pollen collection and weather conditions*

The figures given in each case for flower opening and anther dehiscence in Table 6 are hourly totals for all days when observations were made, and though decided differences in timing are evident between the various plant species they are not so clear cut as when individual days are considered. The peak time of flower opening or anther dehiscence for most of the plants examined was found to vary from day to day by 1–2 hr. and comparison of the hourly figures for the same species on two or more days showed a highly significant difference in timing, probably caused by weather conditions (see χ^2, Table 9). If observations had begun sufficiently early in the morning, the same results would in all probability have been obtained from *Papaver rhoeas* and *Brassica alba*.

These timing differences within a species are, however, small when compared with the differences between species and are not incompatible with the general conclusion that there is a definite time of day when pollen from a particular plant species is available.

The influence of certain weather factors was studied in more detail in the case of red clover. Daily counts of the total number of flowers opening on 20 inflorescences were made throughout August 1946, a succession of young inflorescences being used and counts made on each for 2 or 3 days. Highly significant correlation coefficients were

obtained between the average numbers of flowers opening per inflorescence and both the maximum daily temperature (0·84, $r = <1\%$ P) and the logarithms of the total numbers of red clover loads collected by colonies E4 and K5 (0·86, $r = <1\%$ P and 0·85, $r = <1\%$ P). Highly significant correlation coefficients were also obtained between the logarithms of the number of loads collected by the two colonies and the maximum temperature (0·73, $r = <1\%$ P and 0·75, $r = <1\%$ P). Calling x_1 and x_2 the logarithms of the daily total number of red clover loads collected by colonies E4 and K5 respectively, y the average number of flowers opening per inflorescence and z the maximum temperature, a regression was taken out on y and z and the following regression equations obtained:

$$x_1 = 0{\cdot}21y + 0{\cdot}00z,$$

$$x_2 = 0{\cdot}18y + 0{\cdot}03z.$$

It appears therefore that the effect of temperature on the collection of red clover pollen by these two colonies is negligible compared with the effect of flower opening, or in other words that temperature, at that time of year, influences the pollen collecting of the bees mainly through its effect on the flowers. Temperature was the most obvious factor influencing flower opening, but no others have been examined, it is therefore possible that there is some other basic factor, correlated with both maximum temperature and flower opening. This relation between flower opening and pollen collecting cannot be an entirely straightforward one since three samples of 100 red clover flowers picked on a day when the bees collected little or no pollen at 8.0 a.m., 1.0 p.m. and 4.0 p.m. contained 59, 77 and 53 flowers respectively whose pollen had not been touched.

Table 9. *Differences between days in timing of flower opening or anther dehiscence for five species*

Species	No. of days compared	χ^2	1% point
Trifolium pratense	3	48·5	32·0
T. repens	6	81·5	50·9
Vicia faba	3	68·8	26·2
Ranunculus acris	2	88·8	15·1
Epilobium angustifolium	2	119·7	21·7

Although no direct counts of flower opening were made in this way on white clover, there is indirect evidence that the relation between flower opening and temperature is the same. The whole flowering periods of both clovers (74 days for white and 54 for red) were considered, and calling x the logarithm of the daily number of loads of clover pollen collected, y the relative humidity and z the maximum temperature, regressions were taken out on y and z for the two colonies and both clovers. No significant differences were found between the regression coefficients in any of these four cases and the following average regression equation was obtained

$$x = 0{\cdot}09z - 0{\cdot}02y.$$

This similarity in pollen collection between red and white clover in regard to maximum temperature and relative humidity suggests that the same factors influence the collection of white clover pollen as of red.

5. DIFFERENCES IN POLLEN COLLECTION BETWEEN COLONIES

As stated before, very marked differences were found in 1945 in the relative amount of pollen of different species brought in by the three colonies under examination and continuous trapping from two colonies in 1946 confirmed and amplified these results. The same fact was mentioned by both Todd & Bishop (1940) and Eckert (1942).

Table 10. *Comparison of the number of loads collected by two colonies from various sources*

Plant	No. of loads collected by colony E4	No. of loads collected by colony K5
Salix	392	3,160
Ulex	2,956	701
Buxus	114	809
Aubrietia	483	1,069
Berberis	424	1,653
Betula	0	2,328
Quercus	2,587	79
Ranunculus	4,967	1,507
Vicia faba	4,979	223
White clover	67,444	32,415
Filipendula ulmaria?	8	1,942
Rosa	608	2,008
Papaver rhoeas	1,834	8,066
Epilobium angustifolium	1,735	3,576
Allium?	228	1,387
Red clover	29,386	45,148
Hedera helix	6	2,610

Table 10 gives the yearly totals (1946) for the two colonies of those pollens which show the greatest differences. In nearly all cases these differences were evident on every day throughout the flowering period of the plant concerned. The species are arranged as far as possible in the order of flowering. A tendency for colony K5 to collect most pollen from the spring and autumn plants and colony E4 from the summer plants was quite marked and is partly indicated in these figures. This is illustrated in Fig. 7, where weekly totals of all species of pollen collected by each colony throughout the year are shown.

As a consequence of these differences in seasonal activity by the bees it might be thought that the quantity differences shown in the table were due to this factor alone. That this is not the case, however, can be seen from the fact that a colony which collected only a moderate total amount of pollen by comparison with the other, nevertheless often collected considerably more of one particular species than the other colony. For example, at a time of great pollen-collecting activity by colony E4, which included the collection of *Papaver* pollen, colony

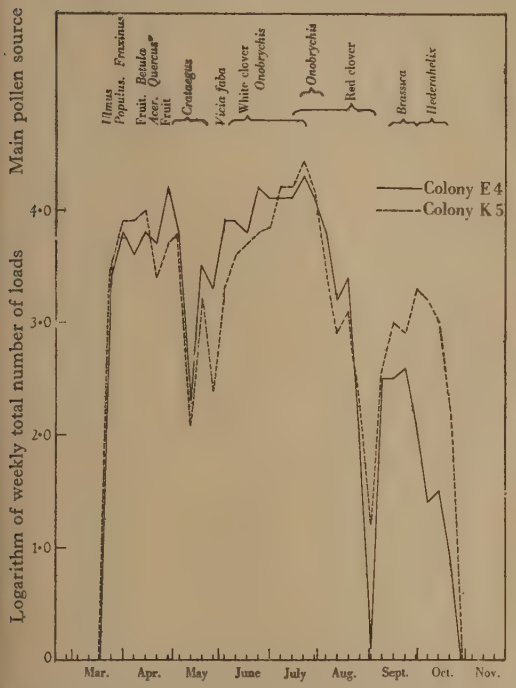

Fig. 7. Logarithm of the weekly total number of pollen loads trapped from colonies E4 and K5 throughout 1946, together with the main pollen sources.

K5 was collecting much greater quantities of this particular species. The same occurred with *Ulex* pollen. Colony K5 gathered less than colony E4, although it was the more actively collecting colony at the time.

It is obvious that qualitative differences on such a scale in pollens collected by different colonies may have very pronounced effects on their well-being, in view of the possible difference in nutritive value of the pollens. Todd & Bretherick (1942) analysed chemically pollens from 34 sources, all except one of which were utilized to a greater or lesser extent by honeybees. They found that the percentage of protein, ether extract, carbohydrate and ash varied considerably, but point out that the nutritive value of these pollens has yet to be determined. Svoboda (1940) tested pollen of hazel (*Corylus avellana*) and fir (*Pinus silvestris*) biologically, and found that the former activated the pharyngeal glands of young bees while the latter did not. He attributed part of this difference to the quantity of digestible albumins present, which formed 26·06% in the case of hazel pollen and 4·28% of fir pollen. In view, therefore, of the probable importance of the fact, it would be of great interest to know why two neighbouring colonies, such as E4 and K5 collected their pollen from different sources.

Possible explanations

(*a*) *Pollen preferences*

It was thought possible that the colonies might exhibit individual preferences for one pollen species rather than another. To test this the bees were offered a choice of pollens over the feed hole. The pollen used was all trapped in 1946 and had been collected by both the experimental colonies. The loads were crushed and placed in circular glass containers, 1 in. in diameter and ½ in. deep. These containers were fixed into holes in a wooden block in such a way that the various pollen species formed a Latin square (or multiple Latin square). In most cases the pollen was taken readily and the bees ate evenly from all parts of the block. In only one case was a significant difference found between the rows and this was quite obviously caused by the brood nest being to one side of the feed hole, as was discovered at the end of the experiment. The block was always removed as soon as the glass at the bottom of any of the containers was visible and each container with its pollen was weighed immediately before and after each experiment. It was found impossible to offer the large numbers of bees present in a colony a sufficient area of pollen to ensure that each bee visiting the block always had a free choice of position, but in the experiments where most pollen was eaten the differences were just as great as those in which less was eaten, so that error due to this cause is probably not great.

Table 11 gives the results of analysis of variance on the seven experiments carried out with the two colonies E4 and K5 and an additional colony Q1 situated in the same apiary. In four out of the five cases where bees were offered a choice of white and red clovers (twice on E4 and once each on Q1 and K5) a highly significant or significant difference was found between the amounts of pollen taken, white clover always being preferred. In the fifth of these

experiments very little pollen of either species was taken. These results were obtained at a time of year when colonies E4 and K5 were collecting pollen almost entirely from red clover, the white clover having been over about a month, and whereas colony E4, during the time that both clovers were in flower had collected more white clover pollen than red, colony K5 had collected more red than white (Fig. 8).

When *Onobrychis* and *Brassica* pollens were included in a block no significant difference in the amount taken was found between these and red clover. *Papaver rhoeas* pollen was included in one block on E4, since this colony had gathered considerably less of this pollen than colony K5 (Fig. 9), but again no significant differences in amount taken between this and the other pollen was found.

The conclusion drawn from these results is that while certain preferences appear to exist, they are common to bees in general and are not the direct cause of the observed differences in pollen collecting between colonies E4 and K5, though they may have an effect indirectly through causing competition to be more severe on some plants than others. It should be pointed out that the pollens used were collected by the bees and not by hand, so that a certain amount of nectar or honey was included, which may have influenced the results. A further limitation in using bee-collected pollen is that the choice is necessarily restricted to those pollens which the bees actually collect in some quantity, whereas it would be interesting to offer them pollens that, though plentiful, they do not appear to use to any extent, such as those from *Tilia* and the Gramineae.

(*b*) *Influence of early morning sunlight*

Very little is known of how the foragers from a colony become allotted to any particular crop, or how the change-over from a failing to a fresh source of pollen is effected, and these matters obviously have a bearing on the question of the cause of differences in pollen collection between colonies. One factor involved is possibly the time of day at which a colony starts work, taken in conjunction with the times at which different pollens are available. The two colonies E4 and K5, although only 55 yd. apart, were so situated in relation to two ash trees on the east side of the apiary that when these trees were in leaf the shadows fell in such a way that the sun always struck K5 at the same time each morning (8.15 a.m. G.M.T.) but E4 was shaded for a longer period varying with the season and becoming progressively shorter from the spring equinox to the summer solstice, though even at that date the sun did not strike the hive until 9.0 a.m. (G.M.T.), ¾ hr. later than K5. Such a difference must have meant that on the whole bees from K5 started work earlier in the morning than those from E4 and it is suggestive, though no more, that colony K5 tended to collect the most of the pollens that become available early in the morning (e.g. *Epilobium* and *Papaver*) while colony E4 tended to collect most of the pollens made available later in the day,

Table 11. *Results obtained from feeding different pollens arranged in a Latin square to colonies of bees*, 1946

Experiment	Hive	Dates	Replicates	Treatments	Means (g.)	Standard error of mean difference
1	E4	10–17 June	8	*Ranunculus*	1·21	0·45
				Vicia faba	1·18	—
2	E4	21–25 Aug.	4	White clover	3·8007	0·1822
				Red clover	2·9257	—
				Onobrychis	2·6873	—
				Brassica	2·7345	—
3	E4	27–30 Aug.	8	White clover	3·7192	0·2766
				Red clover	2·0322	—
4	K5	28 Aug.–4 Sept.	8	White clover	1·6863	0·3389
				Red clover	0·9334	—
5	K5	5–10 Sept.	8	White clover	0·5078	0·1871
				Red clover	0·7208	—
6	Q1	11–16 Sept.	8	White clover	1·3689	0·1404
				Red clover	0·1487	—
7	E4	11–18 Sept.	3	*Onobrychis*	1·2342	0·3990
				Brassica	0·8266	—
				Papaver rhoeas	1·7048	—

primarily legumes. Also it can be seen from Fig. 7 that the weekly totals for colony K5 were higher than those for colony E4 in spring and autumn at which time the colony had 1½–2 hr. more early sunshine, whereas during the summer when legumes were the main pollen source the totals for colony E4 were usually the higher.

(*c*) *Other factors*

It seems probable that differences in the pollen collected by colonies are due to a complex of factors covering both the internal economy of the colonies and the external relationships of their foraging bees. In the former category may come such factors as the demand for pollen, perhaps depending on the larval population and the stored reserves at any time; here also the method of organization of the field force for gathering pollen nectar and water will be important. About all these questions very little is known. In the latter class are included those factors examined in this paper which relate to the behaviour of flowers and the aspect of hives. Other factors of this type are concerned with the relationship between the amount of available pollen and competition from other pollen-gathering insects. All these factors will be affected by general climatic conditions.

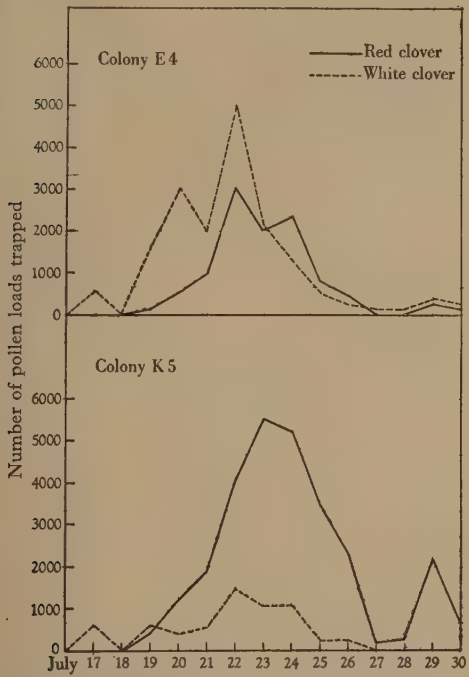

Fig. 8. Number of red and white clover pollen loads trapped from colonies E4 and K5 during the period in July 1946 when both clovers were in flower.

6. SUMMARY

1. The pollen brought in by colonies of bees at Rothamsted during 1945 and 1946 has been collected daily by means of pollen traps and analysed into its constituent pollen species. Approximately 100 plants were found to be used for pollen collection. Legumes (54%), rosaceous trees and shrubs (15%), and forest trees (11%) were found to yield about 80% of the total pollen for 1946. The seasonal occurrence of different pollens has also been analysed.

2. The floral mechanism making pollen available to the bee has been investigated for red and white clover, *Vicia faba*, *Papaver rhoeas*, *Epilobium angustifolium*, *Ranunculus*, *Brassica alba* and *Crepis*, and the connexion between the time of day at which pollen from these plants is available and the time of its collection by bees demonstrated.

3. A correlation has been found between the number of loads of red clover pollen gathered by

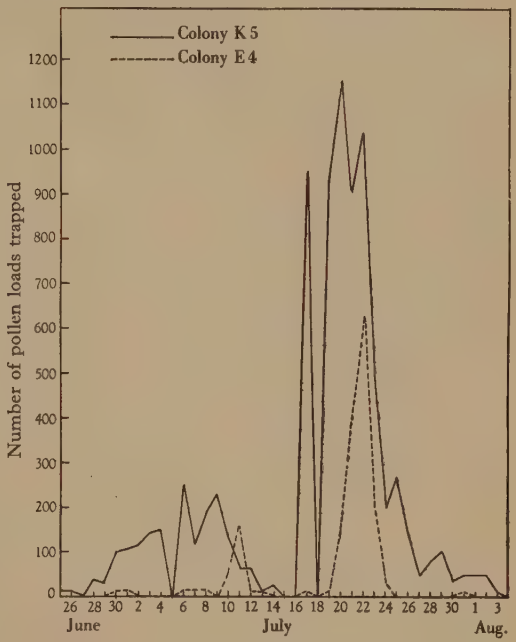

Fig. 9. Number of *Papaver rhoeas* pollen loads trapped from colonies E4 and K5 during July 1946.

bees and the daily maximum temperature, and this has been shown to be due mainly to the increased number of red clover flowers opening at higher temperatures.

4. Large differences in the amounts of pollen gathered from different plant species were found between two neighbouring colonies in the same apiary.

5. A preference for white clover, rather than red clover, *Brassica*, *Onobrychis* or *Papaver* pollen was shown by three colonies, offered a choice of pollens within the hive.

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THE NATURAL CONTROL OF POPULATION BALANCE IN THE KNAPWEED GALL-FLY (*UROPHORA JACEANA*)

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(With 11 Figures in the Text)

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PART I

1. INTRODUCTION

In this contribution to insect ecology the theory of balance of animal populations, formulated by Nicholson (1933) and Nicholson & Bailey (1935), is used for the first time in the interpretation of the results of a field survey. The conclusions are sufficiently striking to claim the attention both of ecologists and economic zoologists, and their importance goes beyond that of the insect material on which they are based.

It is now more than twenty years since Lotka published his mathematical studies on the interaction between predators and prey which were applied by Gause (1934) to the oscillations in the population densities of protozoan predators and prey under constant environmental conditions *in vitro*. Nicholson & Bailey's formulation of the simpler situation which arises when a specific insect parasite and its host have synchronized generations was first shown to apply under idealized laboratory conditions by the neat experiment of de Bach & Smith (1941), where the oscillations in the population density of parasite and host agreed excellently with the theory over a period of eight generations.

The present work provides the first attempted confirmation from field data of the basic assumptions of the theory of Nicholson & Bailey. The theory is subsequently used to interpret the interaction between the various factors destroying the knapweed gall-fly. The quantitative effect of each factor can be examined separately. The clarification of a complex situation achieved in this way may provide the economic entomologist with a new and powerful technique. And the rather paradoxical nature of the conclusions reached may well revolutionize the methods of assessing the probable value of different projected control measures to be applied to insect pests.

If the cause operating to produce balance in the population density of a species is known to be a parasite, workers seeking either to reduce, conserve, or increase the population density of the species can use Nicholson & Bailey's theory to investigate the long-term effects on the balance which may be expected from any alteration of conditions.

The knapweed gall-fly, *Urophora jaceana* (Hering)* (Diptera, Trypetidae), is a member of a large and complex insect community which lives in the flower-heads of the black knapweed *Centaurea nemoralis* Jordan (Compositae). Owing to a happy series of peculiarities in its life history, the gall-fly provides particularly suitable material for the study of population problems in the field.

The problem considered here is formulated thus: What factors control the population density of *Urophora jaceana* in nature, and how do they operate?

Nicholson (1933, p. 135) states that 'a controlling factor should act more severely against an average individual when the density of animals is high, and less severely when the density is low. In other words, *the action of the controlling factor must be governed by the density of the population controlled.*' Controlling factors, with or without the help of other factors, can therefore maintain a species in a state of balance at such an average population density that over a period of years these factors kill the surplus population. Where other factors permit its survival it is the controlling factors which mainly determine whether a species shall be rare or common.

Two groups of controlling factors can be distinguished. The first have been termed *density dependent factors* by Smith (1935). They may be recognized by the fact that at any time the severity of their action increases as the population density rises. Intraspecific competition for limited food supply or limited space operates in this way, and the sigmoid population curves obtained by Pearl (1925) for *Drosophila* cultures, and by many subsequent workers for other species, are explicable on this view (see Crombie, 1945). According to Nicholson's theory, limitation of host population density acts in the same way on the increase of parasites and predators. However, the parasites and predators also exercise a reciprocal influence on the numbers of the species on which they feed.

This reciprocal reaction provides a second type of controlling factor, to which it is proposed to apply the new term *delayed density dependent factor*. A parasite acts as a delayed density dependent factor if its fecundity or its effective rate of increase is strongly correlated with host density. Nicholson

* Until 1937 the knapweed gall-fly was known in this country as *Urophora solstitialis* (L.), but it had long been known that continental *U. solstitialis* was usually a gall-fly of thistles. However, gall-flies bred from the continental knapweed *Centaurea jacea* were found to differ from the thistle species, and were described as new by Hering (1935) under the name *jaceana*. Collin (1937) has found that the British specimens from knapweed are in fact *jaceana*, and not *solstitialis*.

The generic name of the knapweed gall-fly is a point of dispute. Collin (1937) follows Hendel (1927) in accepting the genus *Euribia* Latreille 1802 as valid. This is closely bound up with the very vexed question of the validity of Meigen's 1800 names, of which *Euribia* is one (see Collin, 1946).

Both Séguy (1934) and Kloet & Hincks (1945) accept the genus *Urophora* of Robineau-Desvoidy 1830, and they are followed here. So it comes about that the knapweed gall-fly was called *Urophora solstitialis* (L.) by Varley & Butler (1933), *Euribia jaceana* Hering by Varley (1937*a*, *b*, 1941), and *Urophora jaceana* (Hering) in this present paper!

assumes that if the host density rises above the density of the steady state in which host and parasite are in equilibrium, the *percentage* of hosts destroyed by the first parasite generation will not increase, but remain unchanged. The *number* of hosts killed, and therefore the number of parasites emerging in the next generation, will be proportionately greater. Only after this delay of one generation will the increased parasite population begin to destroy a greater proportion of hosts. Eventually after two or more generations the host density will be reduced. This fall in host density will in turn be followed by a fall in parasite density, which will allow the hosts to increase once more. These oscillations are essentially similar to those predicted independently by Lotka (1925) and Volterra (1926, 1931) (for more complete references see Thompson, 1939). They have been observed experimentally by de Bach & Smith (1941).

In order to find how the mortality factors control the population density of the knapweed gall-fly the following programme of work has been carried out. The natural rate of increase of the gall-fly has been measured under field conditions, and the factors which influence this have been studied. The mortality due to all causes has been assessed, and an examination made to determine which are density dependent factors, and which delayed density dependent factors. The interaction between these factors and the other agencies which cause mortality has been considered in the light of Nicholson's theory of balance of animal populations.

2. THE CENSUS

A site near Madingley, at the edge of the University Farm some 3 miles west-north-west of Cambridge, was chosen for the census work. Knapweed grew in profusion on either side of a grassy cart-track with wide uncultivated verges. The plant community was not stable, as the ground was being colonized by bushes of hawthorn (*Crataegus*). Poplar (*Populus*) suckers, rose (*Rosa*), and bramble (*Rubus*) grew thickly in places. The bushes were cut back in 1932 and again in 1937.

Selected specimens of knapweed from the census area were all identified by Dr W. B. Turrill as *Centaurea nemoralis* Jordan, which was formerly included under *C. nigra* L. The shoots of the knapweed appear above the ground in April and May, and the flower buds appear from amongst the ensheathing leaves in late June and July. They are then 3 mm. in diameter, and increase to between 8 and 12 mm. before the bracts part and the purple florets come into bloom. The growth changes in the flower-heads during the early summer are shown in the diagrammatic sections in Fig. 3. There are about 80 (20–100) florets in each flower-head. Within a few days of coming into bloom the florets shrivel and dry up, and finally their remains fall off in a lump, leaving the ripening fruits behind. The fruits, when ripe, get squeezed out as the bracts dry and contract. Towards the end of the summer some of the flower-heads fall to the ground. As the winter advances more and more flower-heads fall, until in the following June less than a third of them remain on the dry and bleached stems.

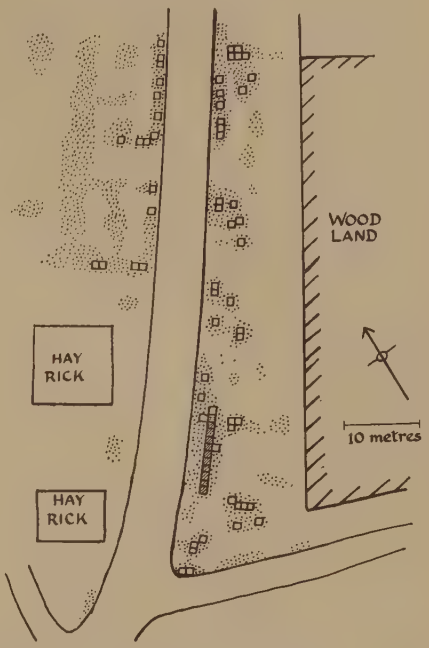

Fig. 1. Sketch map of the census area, showing the distribution of the knapweed (stippled area) and the position of the square metre plots. The stippled square metre was sampled twice in different years, and the cross-hatched square metres were sampled three times.

In the census a total of 92 sq.m. samples were taken from a strip 30 m. long to the west and 70 m. long to the east of the cart track (Fig. 1). In February 1935, 10 sq.m. were collected. More were taken in early June, and from the end of June until the end of October samples were collected at weekly intervals, and a total of 46 sq.m. were cut in the year. In 1936 the weekly routine was begun in early May, and continued to the beginning of October.

The sample squares were not selected at random. Fig. 1 shows that the knapweed was patchy in its distribution, and random samples would frequently have contained little or no knapweed. The sample squares were selected so that all had a fair quantity of knapweed in them. This had two effects: it

reduced the variation between the individual samples, and increased the total quantity of knapweed examined, and hence increased the accuracy of the observations. Had the object of the work been to obtain a valid mean population density per unit area this would not have been admissible, but what was required was a series of comparable samples of the greatest possible homogeneity, and containing the greatest possible amount of material.

Those flower-heads on the standing stems could all be collected without any difficulty. As very few flower-heads fell to the ground by October, the census of the fresh flower-heads up to this time is complete. During the winter a large proportion of the flower-heads fall to the ground, where they soon decay and disintegrate, and cannot be accurately counted. However, though the flower-heads may fall to pieces, many galls remain, and these may be discovered in some numbers by thorough search. The search for fallen flower-heads and galls usually occupied between 1·5 and 2 hr. for each square metre. All the vegetation was cut down and examined, and the ground was teased over with forceps, and the decayed grass and leaves were removed until the ground was bare. Few galls on the surface could have escaped detection. Some, however, were found partly covered in worm castings, and others must have been buried in this way. The ground was also tunnelled both by moles and mice, and a few galls must have been buried by their spoil heaps. Thus it is certain that some of these galls escaped discovery, and the census is correspondingly incomplete. This is discussed below under the heading 'winter disappearance'. It amounted to 60% of the galls in the winter of 1935–6.

Another sampling procedure was used in February 1935, and again in September 1935 and October 1936, when the same line of ten adjacent sample squares was taken, without any search for fallen flower-heads. The variation in the amount of knapweed in these samples was rather greater than in those selected according to the first-mentioned sampling procedure.

All the material collected in the census was removed to the laboratory for examination. This introduces an error into the work, since the density of the population was thereby reduced, thus affecting somewhat the course of events under observation. But the effect was probably small with respect to the inaccuracies arising from sampling errors, since the area sampled in each generation of the flies was a small fraction of the total area inhabited by the flies. Samples were taken from three generations of galls. 21 sq.m. were sampled before the emergence of the adult gall-flies in 1935, but in the first thirteen of these samples no fallen flower-heads were taken. The next generation of galls was removed from 46 sq.m. before they in their turn produced adult flies in July 1936. The removal of the next generation of galls from 35 sq.m. would have no effect before the census had finished. Fig. 1 shows that the site on which the census was made included about 500 sq.m. on which knapweed was abundant, so that the removal of 21 and 46 sq.m. respectively in the two generations amounts to only about 4 and 9% of the total. This effect would have been reduced if the samples had been collected from a larger area. But another error would then have increased, since the percentage of galled flower-heads varied locally within wide limits, and was considerably less only a few hundred yards from the site of the census. Even within the census area the number of gall-fly larvae in each sample area varied so greatly that the mean number per square metre had a standard error equal to at least 15% of the mean. It is improbable that the systematic errors arising from the census method employed are as large as this, so that their effect can be neglected over the small number of generations studied.

Examination of material. Each of the 17,492 flower-heads of the knapweed collected on the 92 sq.m. samples was split open and the contents were examined. Special attention was paid to the knapweed gall-fly, *Urophora jaceana*, and to those other species in the community which were known to affect its numbers (Table 1, Fig. 2). All stages of these were counted as accurately as possible. Certain other species, such as *U. quadrifasciata*, the various Cecidomyiids, and mites, were not counted accurately, since they had little or no direct effect on the numbers of *U. jaceana*.

Treatment of census data. Since the census has been restricted to samples of the whole population, the data are subject to sampling errors. Throughout this work numerical data have been treated statistically. Whenever mean values have been used the standard errors of the means have been calculated by the methods of Fisher (1934) or Bond (1935).

3. THE LIFE HISTORY OF THE KNAPWEED GALL-FLY

The life history of this species was first studied in detail by Wadsworth (1914), and the early stages have been redescribed by Varley (1937*b*). Here only the salient features of the life history need to be mentioned.

The adult gall-flies (Fig. 3 A, B) emerge from the flower-heads of the previous summer in July, and are to be seen in the field for about a month. The liberation of marked flies showed the mean life-span of a female fly to be about a week, but both in the field and in the laboratory certain individuals lived much longer than this.

Table 1. *List of the most important insects forming the community in the flower-heads of the black knapweed* (Centaurea nemoralis) *in the census area at Madingley*

The order of magnitude of the larval population density of the species is indicated by the symbols:

A = abundant, more than 100 per sq.m.
C = common, 10–100 per sq.m.
S = scarce, 1–10 per sq.m.
R = rare, less than 1 per sq.m.

Synonyms are put in brackets

Plant-feeding species	
Diptera, Trypetidae (gall-flies)	
Urophora jaceana (Hering) (*U. solstitialis* Auctt., nec Lin.)	A
U. quadrifasciata (Meigen)	C
Chaetorellia jaceae (Rob. Desv.)	S
Chaetostomella cylindrica (Rob. Desv.) (*C. onotrophes* (L.))	R
Diptera, Cecidomyiidae (gall-midges)	
Dasyneura miki (Kieffer)	A
Clinodiplosis cilicrus (Kieffer)	C
Lepidoptera, Tinaeoidea	
Metzneria (*Parasia*) *metzneriella* (Stainton)	S
Lepidoptera, Tortricoidea	
Euxanthis straminea (Haworth)	R
Eucosma hohenwartiana (Schiff.) (*E. scopoliana* (Haworth))	C
Parasitic species	
Hymenoptera, Chalcidoidea	
Eurytoma curta Walker	C
*E. robusta** Mayr	S
Habrocytus trypetae (Thoms.)	C
*Torymus cyanimus** Boh.	S
Macroneura (*Eupelmella*) *vesicularis* (Retz.)	S
Tetrastichus brevicornis† Nees	R
Tetrastichus sp. B	S
Aprostocetus daira‡ (Walker)	R
Hymenoptera, Braconidae	
Neochelonella (*Chelonus*) *sulcata* (Jurine)	S
Macrocentrus nidulator (Nees)	S
Hymenoptera, Ichneumonidae	
Omorga ensator (Grav.)	R
Ephialtes buolianae Hartig (*Scambus depositor* var. Roman)	R
Glypta longicauda (Hartig) (*G. nigrotrochanterata* Strobl.)	S
G. vulnerator Grav.	S
Predatory species	
Diptera, Cecidomyiidae	
Lestodiplosis miki Barnes	C

* Not listed by Kloet & Hincks (1945). Recorded from *Urophora cardui* in Britain—see Blair (1931).

† Not listed by Kloet & Hincks (1945): apparently this is the first British Record.

‡ Put in the genus *Tetrastichus* by Kloet & Hincks; but according to Mr J. F. Perkins *daira* Walker is an *Aprostocetus*.

Oviposition usually starts on the third day after emergence and continues until the fly dies. When a female fly finds an unopened flower-head of knapweed which is between 3 and 5 mm. in diameter it walks on to it, and turns around a few times. Eventually the fly pushes its ovipositor down at the side of the flower-head and inserts the tip between the bracts. Often the ovipositor is removed after a few seconds and replaced in a slightly different position, but finally the fly remains motionless for about 2 min., and during this time a few eggs are laid. The slender end-piece of the ovipositor is driven through the soft tissue at the base of the flower-head and turns upwards so that the eggs are laid in the space between the florets and the overlapping bracts. The track of the ovipositor is faintly indicated in Fig. 3C.

The eggs are easily seen if a flower-head is split open. They are usually in groups of two or more. A few days after they are laid their discovery is aided by the shrivelling, or retardation in growth, of the florets in their immediate neighbourhood (Fig. 3D). The first larval moult takes place in the egg and the eggs hatch as second instar larvae about 12 days after being laid. The time of hatching depends partly on the temperature, and there may be a difference of 2 or 3 days between the hatching of the first and the last egg of a single batch.

The second instar larva when first hatched creeps over the florets and eats its way into one of them, leaving a small hole with a brown edge, and slowly burrows down the axis of the floret to the ovary. Then almost at once the plant tissue surrounding the ovule swells and elongates, becoming eventually a pear-shaped fleshy mass about 7 by 3 mm., in which the larva lies (Fig. 3E). If two or more adjacent florets contain larvae they fuse together to form a multilocular gall with each larva in a separate cell (Fig. 3F). In time the outer wall of the gall cell hardens and becomes woody, while the inner tissues remain fleshy and are eaten by the larva. The passage by which the larva entered the ovary remains open, so that the cell is finally flask-shaped with a rather wide opening at the top (Fig. 3G). The details of gall formation have not been studied, since they have no bearing on the problem in hand.

The third instar larva appears some 3 weeks after oviposition, and a fortnight after this the hind-end of the body becomes pigmented and sclerotized, and forms the perispiracular plate. As the larva feeds head downwards, this hard black plate forms a plug which usually fits tightly into the neck of the flask-shaped gall-cell. This is important in connexion with the attacks of parasites, described later. The larva is fully grown soon afterwards, and remains inactive in its cell during the winter.

Pupation begins in May when the larva reverses its

position in the gall-cell so that its head faces the exit, and the larval cuticle becomes a hard brown puparium. Within this skin there develops first a fourth instar larva, or prepupa, and then the true pupa, as described for the related genus *Rhagoletis* by Snodgrass (1924). From the puparium the adult fly emerges in about a month, in the early part of July.

The following important features in this life history have made the *Urophora jaceana* particularly suitable for detailed ecological study:

(1) All but the brief adult life is spent within a single flower-head of the knapweed.

(2) The young larvae cause the formation of hard durable galls. Each gall-cell is isolated from the others in the same flower-head. From examination of the galls, the number of larvae which caused their formation can be found. The number surviving can be counted, and the cause of death of the others can usually be inferred from the contents of the gall-cells.

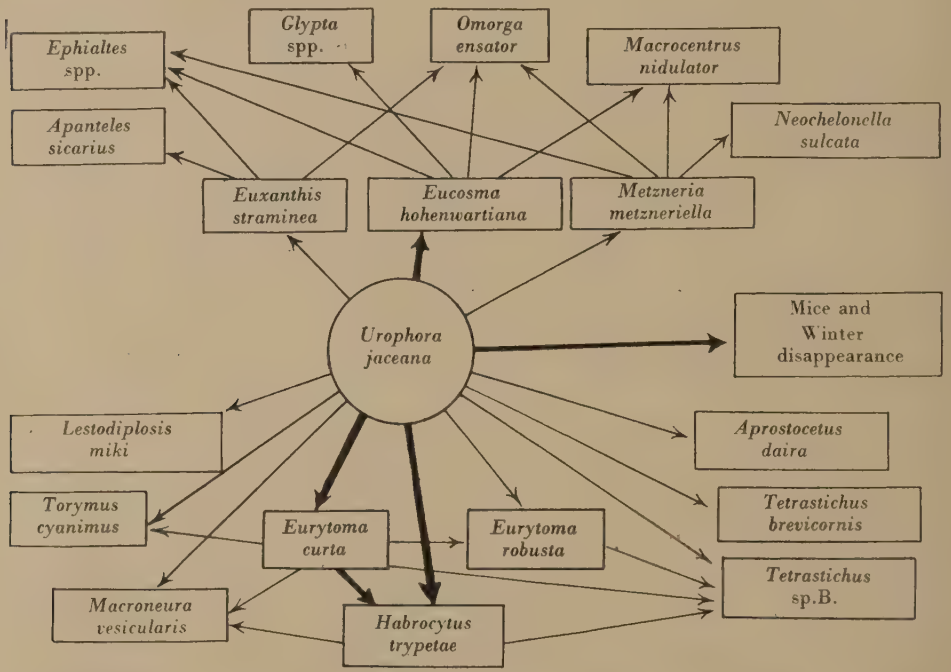

Fig. 2. Food chain of the species which affect the numbers of the knapweed gall-fly, *Urophora jaceana*.

Explanation of Fig. 3

Fig. 3. The knapweed gall-fly and its life history. A. Knapweed gall-fly, male (× 12). B. Knapweed gall-fly, female (× 12). C. Knapweed flower-head, 5 mm. in diameter, with small florets. It contains four gall-fly eggs. Note the faint track of the gall-fly's ovipositor (× 6). D. Knapweed flower-head, 6 mm. in diameter, showing florets half grown. Four eggs have already hatched, and two larvae are shown inside separate florets. Two eggs have failed to hatch. Note that the florets near the track of the fly's ovipositor are stunted in growth. E. Knapweed flower-head 8 mm. in diameter. Most of the florets are almost ready to bloom. A gall, surmounted by the remains of the pappus of the fruit from which it has been formed, contains a second instar larva. The dark woody layer of the gall is beginning to form. F. Knapweed flower-head in bloom. The gall contains third-instar larvae which have already consumed a large part of the fleshy gall-tissue. G. Knapweed flower-head after flowering, in September. The fruits have dropped out, leaving only the paraphyses. The gall is hard and woody, and contains (left) a fully fed gall-fly larva, (centre) a larva of the chalcid parasite *Torymus cyanimus*. On the remains of the host can be seen three egg shells of *Torymus*. On the right is a brown gall-fly puparium containing a larva of the chalcid parasite *Eurytoma curta*. To the extreme left is a slightly swollen fruit containing a larva of the small gall-fly *Urophora quadrifasciata*.

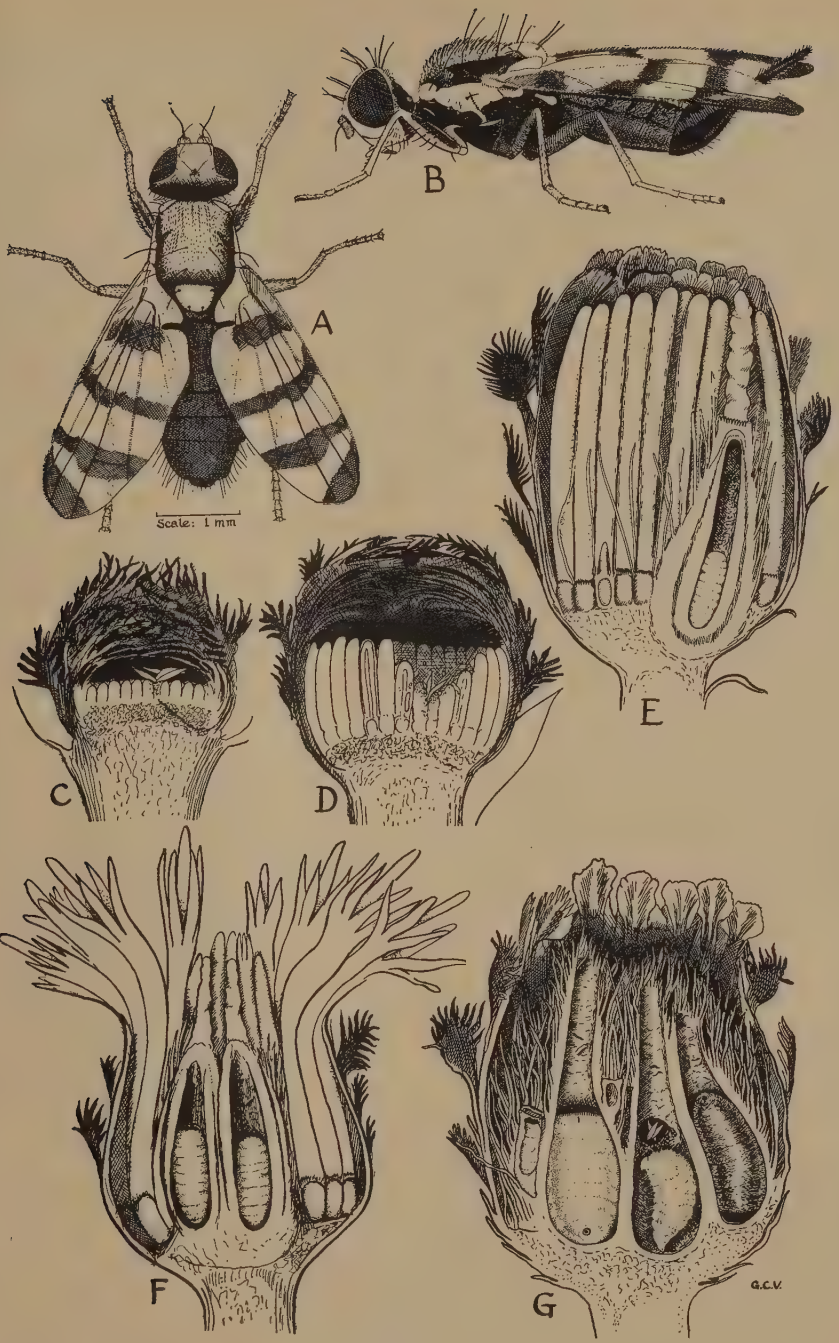

Fig. 3.

(3) There is only one generation in the year. Although the successive stages of development of the gall-fly overlap in time during the summer, equivalent stages of successive generations do not overlap. Hence a complete census can be made for each generation.

PART 2

THE FACTORS WHICH AFFECT THE ADULT GALL-FLIES AND THEIR FECUNDITY

Provided there is no migration, the population density of adult gall-flies in a particular area will change from one generation to the next by a factor equal to the *fecundity* multiplied by the *proportion of females*, and by the *fraction of the eggs which reach the adult stage*. These three quantities must be estimated, and an assessment made of the factors which influence them.

Fecundity has been studied from three aspects. First, the fecundity of the gall-flies in the field has been estimated from the census data. Secondly, it has been studied in the laboratory, and its dependence on nutrition and on certain climatic factors measured. Thirdly, detailed field observations have indicated how oviposition is affected by weather conditions.

1. The fecundity of the gall-flies in the field

No direct measurement of the fecundity was practicable in the field, but the census provided an indirect method of estimation. This is based on the relationship (which has also been used by Sachtleben (1927) in his detailed study of the moth *Panolis flammea*)

$$\text{Mean fecundity} = \frac{\text{No. of eggs laid per unit area}}{\text{No. of females emerged per unit area}},$$

which is accurate if migration can be neglected. It is shown later that the gall-flies move so little that the accuracy of the relationship is not likely to be seriously affected.

The fecundity of the gall-flies in 1935

(*a*) *The number of female gall-flies which emerged per sq.m.* was estimated by counting the number of live or empty puparia in the year-old galls in and after July. There was considerable pupal mortality due to parasites in June, but this had virtually ceased in July, and in 10 sq.m. collected in July and August totals of 9, 6, 6, 0, 6, 5, 3, 17, 13 and 4 puparia were found, 12 of which were about to produce gall-flies, while the other 57 had already done so. This gives a mean of $6{\cdot}9 \pm 1{\cdot}6$ gall-flies emerged per sq.m. in July 1935. The completeness and accuracy of the census data on which this estimate is based are discussed below under the heading 'winter disappearance'.

The proportion of females was estimated from the number of male and female gall-flies which emerged in the emergence cages in the laboratory. Out of 662 gall-flies, 281 were females, or $42{\cdot}4\% \pm 1{\cdot}9$.

Hence the number of female gall-flies which emerged in 1935 is estimated to have been

$$6{\cdot}9 \times 0{\cdot}424 = 2{\cdot}9 \pm 0{\cdot}7/\text{sq.m.}$$

(*b*) *The number of eggs laid per sq.m.* cannot be counted directly, as all the eggs are not present at the same time. The oviposition period lasts about 4 weeks, which is much longer than the time taken to hatch (about 12 days). Empty eggshells cannot be found, and the mortality in the very young larvae would make the sum of eggs and larvae found smaller than the total number of eggs laid. Two indirect methods have been employed to estimate the number of eggs laid per sq.m.

Method 1. It is easy to make a direct count of the late second instar larvae by counting all the gall-cells after the galls have been fully formed. Then, knowing the proportion of eggs laid which successfully form galls, the total number of eggs laid per sq.m. is readily calculated.

All the larvae had formed galls by 13 August, and the number of gall-cells subsequently found in 22 sq.m. was 3247. The mean number of gall-cells per sq.m. in late summer 1935 was $147{\cdot}6 \pm 21{\cdot}5$ (Appendix, Table A, col. 3).

On p. 158 the mortality which occurred up to the formation of the galls is given as $0{\cdot}289 \pm 0{\cdot}022$. Hence the survival up to this time was $0{\cdot}711$, and the number of eggs laid per sq.m. in 1935

$$E = \frac{\text{Gall-cells per sq.m.}}{\text{Proportion of eggs surviving}} = 147{\cdot}6 / 0{\cdot}711 = 208 \pm 31.$$

Method 2. A second method of estimating the total number of eggs laid per sq.m. is to find the mean number of flower-heads per sq.m. which contain eggs, and multiply this figure by the mean number of eggs in each flower-head. Table 6, col. 2 shows that 447 eggs were found in 148 flower-heads, which gives a mean value of $3{\cdot}02 \pm 0{\cdot}15$ for the number of eggs laid per flower-head.

The total number of flower-heads containing eggs cannot be counted directly, since some eggs have hatched before the last have been laid. However, the total number of flower-heads containing eggs or larvae can be counted, and approximates to the total number of flower-heads in which eggs were laid. Although a proportion of the eggs fail to develop, there is only a small chance that none of a group of eggs will survive. A correction can be applied for

any random egg mortality, and allowance made for additional mortality of whole egg batches.

The mean number of flower-heads which contained eggs or larvae of the gall-fly was $60{\cdot}3 \pm 7{\cdot}4$ (Appendix, Table A, col. 2). Of this total a mean of 2·6 contained eggs only, and 57·7 contained larvae already in galls. A figure of 0·29 may be assumed for the random mortality which had occurred before gall-formation (p. 158), and it is seen in Table 6 that for every 886 flower-heads with eggs which form at least one gall-cell there would be expected to be 82·93 flower-heads in which none of the eggs survived to form galls. Hence to the figure of 60·3 flower-heads with eggs and larvae must be added a correction of $(57{\cdot}7 \times 82{\cdot}93)/886 = 5{\cdot}4$, making a total of 65·8 flower-heads per sq.m. which contained eggs of the gall-fly. Since the mean number of eggs laid per flower-head was $3{\cdot}02 \pm 0{\cdot}15$, the mean number of eggs laid per sq.m. in 1935

$$E = 65{\cdot}8 \times 3{\cdot}02 = 199 \pm 23.$$

This second estimate agrees well with that of 208 obtained by the first method. The mean of the two estimates is 203 ± 27. The standard error has been calculated on the assumption that, since the estimates were derived from the same data, the correlation between them is unity. Since the number of female gall-flies which emerged per sq.m. in 1935 was $2{\cdot}9 \pm 0{\cdot}7$, the fecundity in 1935

$$f = \frac{\text{Eggs laid per sq.m.}}{\text{Female flies emerged per sq.m.}} = \frac{203}{2{\cdot}9} = 70 \pm 19.$$

The fecundity of the gall-flies in 1936.

The same methods have been used to estimate the fecundity in 1936.

(*a*) *The number of gall-flies which emerged per sq.m. in* 1936 can be estimated from the data in Table 2. Emergence began late in June as it did in 1935, but cold and wet weather delayed the emergence of some gall-flies until August or September. Further, the rain storms of July caused flooding, which resulted in about 46 % mortality in the puparia. The drowned puparia were not at first easy to distinguish from live ones. Some doubtful puparia were isolated, and one male gall-fly emerged as late as 19 August; some apparently living puparia were found in September. However, in the census no eggs were found after the middle of August, and the last eggs must have been laid by female flies which emerged towards the end of July. The few flies which emerged after this apparently laid no eggs, and so may be neglected.

It is not easy to see from Table 2 what proportion of the larvae and puparia had emerged by the end of July. The fraction which had emerged in sq.m. nos. 57–66, collected between 11 and 28 July, was $24/40 = 0{\cdot}60$. The fraction which had emerged in sq.m. nos. 67–82, collected between 3 August and 2 September, was $34/63 = 0{\cdot}54$. The first of these figures might be expected to be too low, as there were many puparia in these samples yet to emerge. The second figure might be expected to be too high, as it might include some emergence after July. The combined result is likely to be more accurate than either alone, and gives a fraction of emergence $= 0{\cdot}563 \pm 0{\cdot}049$.

The mean number of larvae-plus-puparia in the 36 sq.m. was $3{\cdot}61 \pm 0{\cdot}60$. Multiplying by the fraction of emergence, 0·563, we estimate the number of flies emerging per sq.m. to be $2{\cdot}03 \pm 0{\cdot}38$ per sq.m.

Since the proportion of females in the population was 0·424, the number of female flies which emerged per sq.m. is estimated at

$$2{\cdot}03 \times 0{\cdot}424 = 0{\cdot}86 \pm 0{\cdot}17.$$

(*b*) *The number of eggs laid per sq.m. in* 1936. *Method* 1. The number of gall-cells found per sq.m. in samples nos. 73–92 was 28 ± 5 (Appendix, Table B, col. 3). The total mortality up to gall-formation was $37{\cdot}5\,\% \pm 3{\cdot}4$ (see p. 161) so that the proportion surviving to form galls was 0·625. Hence the number of eggs laid per sq.m. in 1936

$$E = \frac{\text{Gall-cells per sq.m.}}{\text{Proportion of eggs surviving}} = \frac{28}{0{\cdot}625} = 44{\cdot}8 \pm 8{\cdot}5.$$

Method 2. The mean number of eggs laid per flower-head was $267/88 = 3{\cdot}04 \pm 0{\cdot}18$ (Table 7). The mean number of flower-heads containing eggs and larvae in 29 sq.m. was $12{\cdot}3 \pm 1{\cdot}6$ flower-heads per sq.m. (Appendix, Table B, col. 2). However, only 1·4 per sq.m. contained eggs, and 10·9 per sq.m. already contained larvae in galls. Allowance must be made for the mortality of eggs and larvae before gall-formation. It is shown on p. 161 that this mortality appeared to comprise 7·7 % infertility of whole egg batches, followed by a 32·3 % random mortality of the remainder. Correction must first be applied for the random mortality. Table 7 shows that with a mortality of 0·32, for every 289 galled flower-heads there would be 35·5 flower-heads in which none of the eggs laid eventually produced galls. Hence the 10·9 flower-heads containing larvae represent $10{\cdot}9\,(1 + 35{\cdot}5/289) = 12{\cdot}24$ flower-heads which had previously contained fertile egg batches.

If 7·7 % of the egg batches were infertile, this number of flower-heads must be divided by the survival, 0·923, to give a total of $12{\cdot}24/0{\cdot}923 = 13{\cdot}3$ flower-heads per sq.m. with eggs. Adding the 1·4 flower-heads found containing eggs, this gives a total of 14·7 flower-heads per sq.m. in which eggs were laid.

Multiplying this by the mean number of eggs laid per flower-head, we estimate the number of eggs laid per sq.m.

$$E = 14{\cdot}7 \times 3{\cdot}04 = 44{\cdot}7 \pm 5{\cdot}6.$$

The estimates by the two methods agree, and their mean is $44{\cdot}8 \pm 7{\cdot}1$. Hence the fecundity

$$f = \frac{\text{Eggs laid per sq.m.}}{\text{Female flies emerged per sq.m.}} = 44{\cdot}8/0{\cdot}86 = 52 \pm 9.$$

This estimate of the fecundity in 1936 is rather lower than that for 1935, but the difference is not significant.

removed and counted in a drop of water under a binocular microscope.

The first experiment was designed to discover the sizes of flower-heads which were acceptable to the gall-flies for oviposition. Six pairs of gall-flies were isolated in hurricane-lamp glasses over flower-pots filled with damp sand. Flower-heads of the knapweed were provided with their stalks in glass tubes containing water. Each pair of gall-flies was given

Table 2. *The numbers of gall-fly* (Urophora jaceana) *larvae, puparia, dead puparia, and puparia from which flies had emerged in the square metre samples nos.* 47–82, *in the summer of* 1936

Date (1936)	Sq.m. nos.	Live larvae	Live pupae	Flies emerged	Total	Date (1936)	Sq.m. nos.	Live pupae	Dead pupae	Flies emerged	Total
12 May	47	2	.	.	2	28 July	65	.	.	.	0
19 May	48	.	.	.	0	28 July	66	.	.	.	0
26 May	49	1	.	.	1	3 Aug.	67	1	.	1	2
2 June	50	2	3	.	5	3 Aug.	68	.	.	1	1
9 June	51	.	.	.	0	4 Aug.	69	2	.	.	2
16 June	52	.	3	.	3	11 Aug.	70	5	.	5	10
23 June	53	.	2	.	2	12 Aug.	71	.	.	.	0
30 June	54	.	4	1	5	12 Aug.	72	3	.	6	9
7 July	55	.	1	3	4	17 Aug.	73	.	.	1	1
7 July	56	.	2	3	5	18 Aug.	74	1	.	1	2
11 July	57	.	3	.	3	18 Aug.	75	.	.	.	0
13 July	58	.	.	2	2	24 Aug.	76	.	.	1	1
14 July	59	.	3	.	3	25 Aug.	77	.	.	.	0
14 July	60	1	.	2	3	26 Aug.	78	.	1	2	3
21 July	61	1	3	4	8	31 Aug.	79	.	3	1	4
21 July	62	.	3	2	5	31 Aug.	80	.	2	1	3
21 July	63	.	1	10	11	2 Sept.	81	.	4	10	14
28 July	64	.	1	4	5	2 Sept.	82	2	5	4	11
Totals	18	7	29	31	67		18	14	15	34	63
No. per sq.m.		0·4	1·6	1·7	3·7			0·8	0·8	1·9	3·5

Grand total $\Sigma x = 130$,

$\Sigma x^2 = 922$,

$\bar{x} = 3{\cdot}61$,

$36\bar{x}^2 = 470$,

$\Sigma (x - \bar{x})^2 = 452$,

estimated standard error $s = \sqrt{\left(\frac{452}{36 \times 35}\right)} = 0{\cdot}60$.

Emergence in samples 57–82 $= 58/103 = 0{\cdot}563$.

Estimate of standard error $s = \frac{1}{103}\sqrt{\frac{58 \times 46}{103}} = 0{\cdot}049$. Combining the total per sq.m. ($3{\cdot}61 \pm 0{\cdot}60$) and the fraction which emerged ($0{\cdot}563 \pm 0{\cdot}049$) the emergence is estimated at $2{\cdot}03 \pm 0{\cdot}38$.

2. The experimental measurement of fecundity

The gall-flies used in these experiments were reared in an outdoor insectary from larvae collected during the winter. Preliminary work showed that mature gall-flies would oviposit in flower-heads in captivity, even if they were confined in very small glass jars. The eggs, laid in the space between the developing florets and the overlapping bracts, can easily be

either three or four flower-heads of different sizes. The experiment was carried out in a cool greenhouse, in which temperature and humidity were uncontrolled. The flies were fed on sugar solution. After 2 or 3 days the flower-heads were removed, and measured, and the eggs in each were counted.

In every case the majority of the eggs were laid in the smallest available flower-head, whether this was 3 mm. in diameter or as large as 5 mm. Out of a total of 663 eggs laid in this experiment, only 66

were laid in flower-heads whose diameter exceeded 5 mm. Flower-heads smaller than 3 mm. are not suitable, as they are still enveloped in the young leaves of the flowering shoot. This preference for oviposition in flower-heads of 3–4 mm. diameter agrees with the fact that the stage of development of the gall-fly larvae found in the census was closely related to the stage of growth of the flower-head in which they were feeding.

Field observations show that after a gall-fly has laid eggs in a flower-head it walks away and seeks another. The second experiment was planned to see whether the gall-flies laid fewer eggs if provided with only a limited number of flower-heads in which to lay. Five pairs of gall-flies were isolated with 1, 2, 4, 8 and 16 small flower-heads respectively. Other conditions were as in the first experiment. The experiment continued until the death of all the female flies, the flower-heads being changed once during the period of life.

The first gall-fly, provided with a single flower-head, laid 216 eggs. The second laid 277, the third 29 and the fourth 78 eggs, but only lived for 3 days, while the fifth laid 125 eggs. This demonstrates clearly enough that the gall-flies do not restrict their output of eggs when there is only a single flower-head available and in the experiments which follow, each female gall-fly was provided with a single flower-head of suitable size.

(*a*) *The effect of mating on fecundity*

Six unmated female gall-flies were isolated in glass bottles as in Fig. 4A, and the flower-head was removed every 3 or 4 days and examined for eggs, by which time most of them had started development. As controls, six similar females were kept with males, and their performance was compared. The unmated females laid nearly as many eggs on the average as the mated females (22 as against 29), but none of the eggs of the unmated gall-flies developed normally. These results are in agreement with those of Glaser (1923) for the flies *Musca* and *Stomoxys*. The yolks of the eggs laid by the unmated gall-flies remained opaque, shrank away from the egg shell, and became shortened, or constricted in various irregular ways. Eggs of exactly similar appearance were found in the field, and it is probable that much of the egg mortality in the field was due to lack of fertilization.

(*b*) *The effect of feeding on fecundity*

The ovaries of newly emerged female gall-flies are very small, but in a few days they become greatly enlarged and full of ripe eggs, and the flies start to lay eggs. The effect of feeding gall-flies on cane-sugar was tested in the following way.

Female gall-flies, which were less than 1 day old, were taken from the emergence cage and placed in separate glass bottles as in Fig. 4A, each with a male. The bottom of each bottle was covered with damp cotton-wool, and a small glass tube supported on a card held a flower-head of about 4 mm. diameter in a little water. Bottles containing flies were set up every few days as the flies became available, and each day's emergence was divided into two series. In the one the cotton-wool was moistened with a dilute solution of cane-sugar, and in the other, which served as a control, only tap water was given. Temperature and humidity were not controlled. The eggs were counted every day, and fresh flower-heads provided. The female gall-flies were dissected when they died, and the eggs remaining in the ovaries were counted.

Altogether 32 female gall-flies were used in the experiment, but the first eighteen gave unsatisfactory results, as many of them soon died from a fungus disease. The last fourteen gave better results. The unfed flies laid on the average 95 eggs (maximum 149) and lived for about 8 days (maximum 10 days) while the flies fed on sugar solution laid on the average 220 eggs (maximum 316) and lived on the average 23 days (maximum 31 days). These differences are strongly significant, and it is concluded that both the fecundity and the longevity are doubled if the gall-flies are provided with sugar. Feeding did not alter the length of time before the laying of the first eggs, which was about 4 days, nor did it affect the number of eggs which remained in the ovaries at death, which was about 50.

The question arises whether the gall-flies feed in the field. The mouthparts of the gall-fly are similar in a general way to those of the blow-fly (*Calliphora*) (Graham-Smith, 1911) and might enable the flies to feed on liquid food, perhaps including particles in suspension. Experiments on thirsty gall-flies showed that when presented with a freshly made suspension of yeast in cane-sugar solution, the crop contents were devoid of yeast cells. However, Boyce (1934, p. 510) found that the flies of the related genus *Rhagoletis* ingested solid matter, such as diatomaceous earth, if it was mixed with sugar solution and sprayed on leaves.

The only types of food likely to be available to the gall-flies in the field are the nectar of flowers, and the honey-dew of aphids. The flowers in bloom in the census area when the gall-flies are present were wild rose (*Rosa*), various small leguminous species and three kinds of Umbelliferae (wild carrot (*Daucus carota* L.), wild parsnip (*Pastinaca sativa* L.) and hogweed (*Heracleum sphondylium* L.)) of which only the wild carrot was in bloom in the early part of the period. In 1936 all the Umbellifers were in bloom when the gall-flies were common. Of these flowers,

only the Umbellifers were frequented by Diptera. The flower-tables were examined repeatedly, but although there were many gall-flies close by on the leaves and flower-heads of the knapweed, none was seen feeding. However, two males of *Urophora quadrifasciata* were seen on wild carrot in 1935.

Aphids were scarce in the census area in 1935 and 1936, and the gall-flies did not seem to be attracted to them in any way. In 1938 aphids were abundant on the knapweed, and the question of feeding was examined directly by the analysis of crop contents. Fourteen wild gall-flies were dissected soon after capture, and in about half the specimens, both male and female, the crop was distended with a clear yellowish fluid. The crop was placed on a waxed slide and punctured. An equal amount of Fehling's reagent was added, and some of the mixture was sucked into a U-shaped capillary tube, and immersed in boiling water. In all cases the test clearly demonstrated the presence of reducing sugars in the food. It seems likely that honey-dew was the source of the sugar.

To conclude, since both the population density of aphids and the time of the flowering of the Umbellifers are so variable, the food supply is inconstant. Fluctuations in such food supply may alter the fecundity of the gall-flies in the field.

(*c*) *The effect of combinations of temperature and humidity on fecundity*

The precise effect of weather on an insect is difficult to determine, since so many variables have to be considered. However, some information can be obtained on this effect by comparing the behaviour of the gall-flies observed in the field under known weather conditions with the results of laboratory experiments conducted under conditions of constant temperature and humidity.

The laboratory experiments were designed to test the effect of constant temperature and humidity on the fecundity of gall-flies which were already sexually mature, and ready to lay eggs if given the right conditions. Diagrams of the apparatus used are given in Fig. 4. The experimental chambers (Fig. 4A, *e*) were a series of bottles of the same size as used in other experiments on oviposition, and one male and one female gall-fly were put in each. A suitable flower-head of knapweed was put with its stalk in a narrow glass tube containing a little water. Evaporation was reduced as much as possible by removing all the small leaves from the knapweed stalk, and by plugging the open end of the glass tube with cotton-wool.

The temperature of the bottles was kept constant by sinking them in a large tank of water provided with thermostats. In 1935 the temperature control was maintained by a toluene-mercury gas thermostat, and temperatures between 20 and 32° C. were studied. In 1936 a cooling system was installed, in which an electric thermostat operated a relay to a pump which circulated the water through an ice-box. The temperature could be kept constant to within a quarter of a degree C., and temperatures down to 15° were used.

Humidity was controlled by a flow method. The bottles were closed by well-fitting rubber stoppers, and connected together by T-pieces so that a flow of conditioned air could be sent through them in parallel (Fig. 4B). The rate of flow in each bottle was adjustable by a screw clip and was observed in a separate bubbling tube which contained oil of low vapour pressure. The rate of flow was such that each bottle received its own volume of air every 2 min. The source of air was a pump worked by tap water (Cannon & Grove, 1927) and this proved very reliable and easy to adjust. The air was passed through a series of three jars filled with broken glass and strong caustic potash, in which the humidity of the air was determined. In 1935 these jars were kept in a separate water-bath (Fig. 4C) which made possible the adjustment of humidity by alteration of the relative temperature of the two water-baths. In 1936 the whole apparatus was put in the same water-bath (Fig. 4D). The air delivered by these jars could be tapped off at a T-piece and its humidity could be measured by a dew-point hygrometer. The humidity of the air after passage through the experimental bottles could be measured in the same way. The difference in relative humidity never exceeded 5 % and was usually about 3 %.

Light was not controlled, and its intensity was much lower than in the room as a whole owing to the submersion of the bottles in the water tank. However, bright light is not necessary to ovipositing flies, since they were seen ovipositing by weak artificial light.

Newly emerged gall-flies were kept for 3 or 4 days in milk bottles before the experiment; they were fed on dilute cane-sugar solution. This gave time for maturation and mating. The gall-flies were then put in the experimental bottles, each with a suitable flower-head, and the experiment continued until their death. The flower-heads were examined daily, and the eggs laid were counted, and fresh flower-heads substituted. This occupied about 20 min. each day, during which time control of the conditions ceased.

In 1935 only four experimental bottles were used, but this was increased to eight in 1936. The gall-flies were available for study for only about a month in each year, and the effect of only fourteen different conditions was studied, using in all 112 female flies.

This small number, coupled with the great variability in the performance of individual gall-flies, makes the statistical error in the results large. It was impossible to perform the experiments on a larger scale without much more expensive apparatus, owing to the limited time during which gall-flies and flower-heads were available, and also because of the pressure of census work which had to be done at the same period.

Although the accuracy of this physiological study is low, the results given in Table 3 and Fig. 5 show sufficient consistency for the drawing of certain important conclusions. The highest fecundity (77 eggs per female) was recorded at 30° C. and 82% R.H., and the graph indicates that there is an optimal region for oviposition under constant conditions which lies between 22 and 32°. The effect of humidity was too small to be statistically significant, but the results suggest that at any one temperature the fecundity is highest at a humidity of over 60% saturation.

The values for the fecundity in this experiment are all very low, and seem to differ by a factor of three from the results in similar bottles in which the temperature and humidity were not controlled. The difference here might be due to low light intensity, or to some toxic emanation from the rubber (Mellanby & Buxton, 1935), or simply to the constancy of the conditions (see Uvarov, 1931).

The fall of the fecundity at high temperatures is partly due to a reduced length of life. Fig. 6 indicates the effect of temperature on the length of life. The data for the lower temperatures come from Table 3. The effects of subjecting the gall-flies to higher temperatures for periods of 1 hr., or 24 hr., were observed separately in a much simpler apparatus. The effect of a temperature of 44° was severe. The flies appeared to be dead after 1 hr., but at room temperature they all revived, although recovery was often incomplete. At 46° all were dead within an hour. At 37° the flies were active and apparently normal in their behaviour for some hours, but

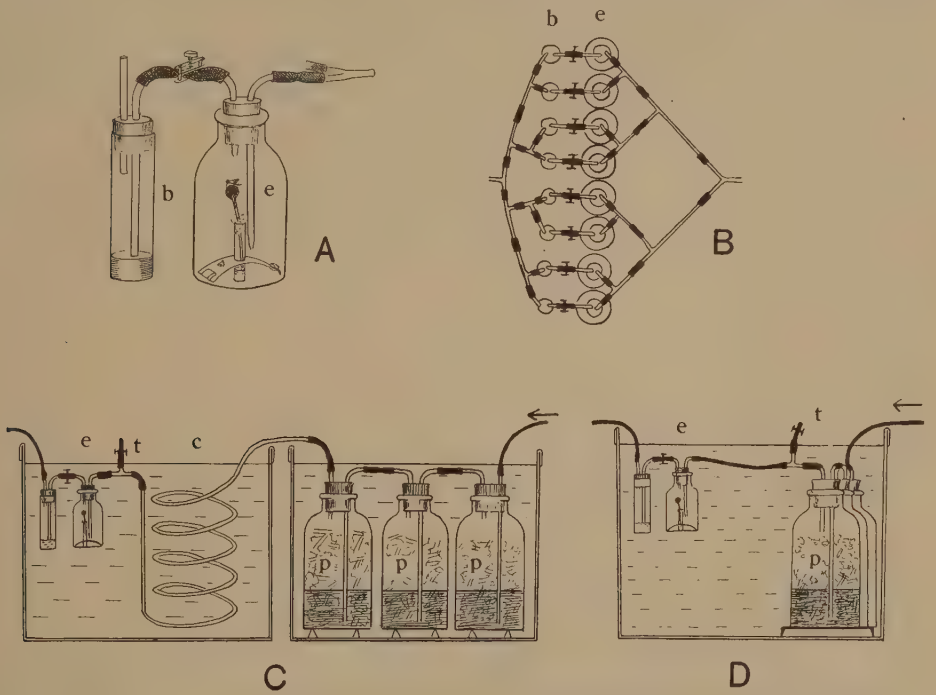

Fig. 4. Apparatus for controlling temperature and humidity. A. Experimental bottle *e* containing a pair of flies and a flower-head of the knapweed, connected to the bubbling tube *b* which contains oil. B. Diagram showing the method of connecting eight experimental bottles in parallel. C. Apparatus as used in 1935; air was led through the potash bottles *p* in the first water-bath, passed through a metal coil in the second water-bath, and then past a tap *t* into the experimental bottles. D. Apparatus as used in 1936.

invariably they died within a day. Similar results were observed both at 100% R.H. and under drier conditions. The fecundity experiment showed that at 35° the mean length of life was about a day, but the gall-flies laid a number of eggs in that time. The highest temperature recorded in the field was 27°.

3. Field observations on the adult gall-flies

The gall-flies were abundant in the field only in July, and at this time of the year there was much census work and laboratory experimentation to be done. However, in 1935 1 day a week was spent in the field on the site of the census, and 3 days a week in 1936. Part of this time was spent in collecting material for the census, and the rest in observing the adult gall-flies.

A field study of the activities of the gall-flies in relation to the varying conditions of the environment cannot give a quantitative estimate of the effect of environmental conditions on the fecundity. But observations of activity, when considered in the light of the results of the laboratory experiments and the census data, lead to certain important conclusions.

(*a*) *The population density of the gall-flies and its bearing on their fecundity*

Chapman (1928) and MacLagan (1932) have shown that the population density of an insect may affect its fecundity; there is an optimum population density, above and below which various factors reduce the number of eggs laid. There is evidence that for at least part of the season the population density of the gall-flies was below this optimum.

The population density was estimated by walking very slowly along the side of the cart track, and counting all the gall-flies seen. The area covered by this search in 1936 was about 100 sq.m., but only about 50 of these contained much knapweed. As the flies spend almost the whole of their time on the knapweed and seldom stay on any other plant for more than a few seconds at a time, it is best to express the density of gall-flies in terms of the total number of flies observed divided by the area containing knapweed. The number of gall-flies seen in 1936 was greatest on 7 July, when twenty males and six females were seen. On 27 July, ten males and four females were seen. Later observations showed two males on 4 August, a male and a female on 10 August, and a single male on 15 August. The maximum density recorded was therefore one fly in each 2 sq.m., and the density fell to one fly in 25 sq.m. by the beginning of August.

This low population density apparently reduces the chance of finding mates. In 1936 the gall-flies were seen in normal coitus some twenty times, while on four occasions interspecific pairing was seen. On 7 July a male of the gall-fly *Urophora jaceana* was seen paired with a female *U. stylata*. This is an easily distinguished species which forms galls in the flower-heads of the spear thistle, *Cirsium vulgare* (Savi) Ten. Males of *Urophora jaceana* were seen

Table 3. *The effect of constant experimental conditions of temperature and humidity on the fecundity and survival of adult gall-flies* (Urophora jaceana)

Temp. (°C.)	Relative humidity (%)	No. of female flies	No. of eggs laid by each female fly (zeros omitted)	Total no. of eggs	Mean no. of eggs and standard error	Mean no.* of days alive
20·4	88	4	21, 96	117	29±33	3
22·4	43	4	4, 133	137	34±33	2·5
24·3	34	4	27, 98	125	31±23	3·2
24·3	85	8†	116, 122, 204	442	55±21	3·5
27·3	40	4	9	9	43±16	1
27·3	40	8†	46, 120, 137, 203	506		
27·3	100	4	43, 47, 120	210	52±25	1
31·4	30	4	77, 90	167	42±26	2
15	40	12	4, 6, 87	97	8± 7	6
15	82	10	16, 17, 21, 40, 110	204	20±11	9
27	53	8	31, 124, 128	283	35±20	3
30	82	15	3, 58, 63, 75, 83, 108, 158, 197, 198, 205	1148	77±21	1·7
35	43	8	97	97	12±12	1·6
35	82	14	13, 47, 87, 95, 116	358	26±11	1
35	100	5	28, 42	70	14± 9	1·5

* This does not include the 3–4 days at room temperature before the experiment began.

† In these two instances each jar contained two female flies, and the total number of eggs laid by the two is recorded.

on 30 June and 10 August paired with females of the smaller and differently marked species *U. quadrifasciata*, which is common in knapweed, but forms no gall. On 10 August a female of *U. jaceana* was found paired with a male of *U. quadrifasciata*.

Only one of these cases was noted in July, and on that day the males of *U. jaceana* greatly outnumbered the females of the species. On the other 3 days the population density of the gall-flies *U. jaceana* was very low. No interspecific mating was seen in 1935 when the maximum population density was more than twice as high as in 1936, and the emergence was more concentrated into the month of July. Interspecific pairing is therefore regarded as a sign that mates of the same species are difficult to find.

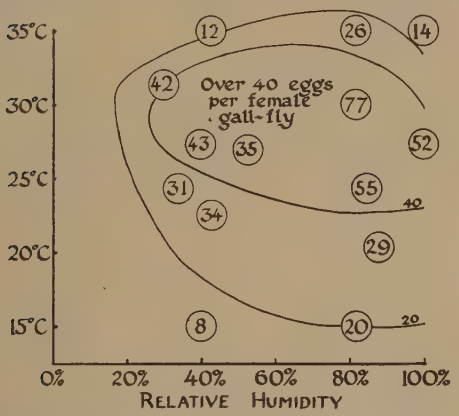

Fig. 5. The effect of constant conditions of temperature and humidity on the fecundity of the gall-fly. The figures in the circles show the mean values for the fecundity under different conditions. The curves show the approximate limits of regions in which the fecundity is below 20, between 20 and 40, and above 40 eggs per female gall-fly. (Data in Table 3.)

Interspecific pairing between related species of tsetse flies (*Glossina* spp.) has been observed in the field by Vanderplank (1947), who recorded no mating preferences.

No attempt was made to get eggs from the gall-flies found cross-mated. But these observations may be correlated with the egg mortality discussed below. Egg mortality was greater in 1936 than in 1935, and in 1936 7 % of the egg batches were infertile, and the eggs resembled those laid by unmated females.

The meeting between the sexes in the gall-flies is not a rapid process, because the movements of the flies are so slow; they seldom fly, and when they do so they rarely fly more than 2 ft., and more usually only 2 or 3 in. Males are usually solitary, and even when they are active they tend to confine their movements within a small area. On 7 July 1936 seven males remained for 10 hr. within a foot of where they were first seen; they were observed at least eight times during this period. The males are pugnacious, and when two males meet they buffet one another with head and vibrating wings, or even grapple together, until one eventually retreats. Boyce (1934, p. 450) describes similar behaviour in the related genus *Rhagoletis*. It is almost as if each male maintains a territory, as do the males of certain birds! The female gall-flies, on the other hand, partly by short flights, but mostly by walking, move distances of a few feet an hour in their most active periods. If a female meets a male during this wandering, courtship and mating may follow. But

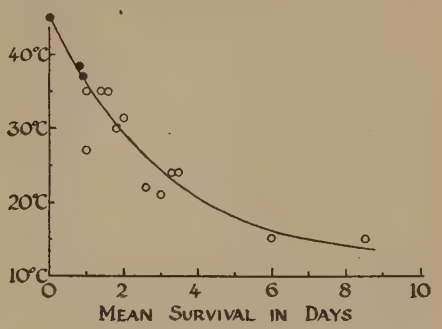

Fig. 6. The effect of temperature on the longevity of adult gall-flies. White circles—data from Table 3; black circles—data from experiments on thermal death point. (The effects of humidity are neglected.)

pairing does not always result from such encounters. A female which was seen walking from flower-head to flower-head met a male. She at once flew a few inches, and went under a leaf where she remained hidden for 2 min.

(*b*) *Experiment on the dispersal of adult gall-flies*

In 1938 four liberations of marked gall-flies were made between 24 June and 1 July, all in exactly the same spot within 2 yd. of the cart-track in the former census area. Each batch of flies was distinguishable by a different mark in 'Robialine' enamel, either on the wing, or more usually on the thorax or abdomen. Altogether 108 flies were liberated, of which 70 were males and 38 were females. They were sought on seven occasions, the last being 13 July. The distance travelled and the type of mark was noted in each case, without the fly being captured. Marked flies were seen on 147 occasions; 107 of the recoveries were of males and 40 of females, so that, allowing for the differences in the

numbers liberated, males were seen about one and a half times as frequently as females.

Counts of the flies only a few minutes after they had been liberated showed that not more than 75% could usually be found. However, in the case of two liberations more than half the flies were still found after an interval of 2 or 3 days, while only just under half were found after 4 days had elapsed. This high proportion of recoveries shows how different the behaviour of the gall-fly must be from that of the related *Rhagoletis* (Phipps & Dirks, 1932), in which 12% recoveries were made, at distances of 38 to 156 yd. from the point of liberation.

Early in the experiment the weather was cold and windy, and dispersal was slow, no flies being found more than 3 yd. from the point of liberation even after 5 days. There followed some sunny days, and of the second liberation of 37 flies 18 individuals were found after 4 days, the most distant male having by then reached a point 9 yd. from the point of liberation. Six days after this liberation 11 of the flies were still found, the furthest having got 15 yd. away. After 14 days one female was found 7 yd. away, and six males were found between 3 and 22 yd. from the point of liberation. After 16 days only two males were found, these being 3 and 20 yd. away respectively. Every day the search was continued far outside the area in which flies were discovered. Curiously enough not a single fly was found to have crossed the grassy cart-track, which was only about 6 yd. wide, although knapweed was abundant on the other side. The marking did not appear to impair the flight of the gall-flies, and they flew readily if disturbed.

The rate of disappearance of the flies is consistent with the hypothesis that about 75% of the flies present were discovered, and that mortality rather than migration accounted for the slow fall in numbers. The figures suggest that after 1 week the number of flies present had fallen to a half, and after 2 weeks to a quarter of the number originally present, which gives an average life of 8–10 days. It is concluded that migration is far too small a factor to invalidate the use of the formulae used to estimate the fecundity of the gall-flies from the census data.

(c) *The effect of weather on the behaviour of the gall-flies*

On all the days in 1935 and 1936 when flies were observed in the field, the weather conditions were noted every hour. The temperature and the humidity were measured with a whirling hygrometer at a height of 4 ft. from the ground, and sometimes also at 1 ft. from the ground. The wind velocity and the amount of cloud were also estimated. These results were compared with continuous records of the temperature and relative humidity measured in an out-door insectary at the Entomological Field Station, 2 miles away.

The highest temperature recorded in the out-door insectary was 32° with a humidity of 38% in July 1935, and the lowest maximum day temperature in July was 15° with 80% humidity. The minimum temperature recorded was 7° with a saturated atmosphere. All these conditions are tolerated by the gall-flies in the laboratory, and the daily maximum temperature was always within the range of conditions in which the gall-flies laid eggs in the laboratory under constant conditions. This is in contrast to the results of Buxton & Lewis (1934, p. 225) on the tsetse flies. These authors found that the maximum recorded temperature reached the upper fatal limit of the flies, and that conditions in the wet season were such that the fecundity of the tsetse flies was reduced to zero.

Although the weather conditions in the census area were always within the range of tolerance of the gall-flies, nevertheless, changes in the weather altered the behaviour of the flies. On 15 July 1935, at 9.30 p.m. G.M.T., a short search was made for flies by lamp-light, and six males and two females were seen resting on the unopened flower-heads of the knapweed. Next morning at 4 a.m. an hourly routine began; a strip of ground to the east of the cart-track was examined carefully and all the gall-flies seen were noted, and their positions were marked by gummed labels stuck to the plants an inch or so away from the flies. If this was done carefully the gall-flies seldom flew away, although they turned and watched the operation. The area searched in 1935 was about 60 sq.m. and it took nearly an hour to cover it. At first the gall-flies moved very little, but, as the morning advanced and the temperature rose, their activity increased, and many flies appeared which had certainly not been in plain view before. By 8 a.m. most of the flies had moved some distance from their labels, and it was not easy to guess which was which, so the labelling was discontinued. The relevant observations are summarized in Table 4. Of the time periods observed, that between 7.43 and 8.43 a.m. was the one in which most gall-flies were seen, and after this they soon began to disappear.

A more complete series of observations was made on 7 July 1936, over an area of about 100 sq.m. which included the area searched in 1935. Table 4 shows that the results were rather similar, but that there was a much greater excess of males. The general activity of the gall-flies was low. No oviposition was observed (though it probably occurred) and many of the gall-flies remained close to their labels for long periods. Two males confined their movements within a radius of only 6 in. of their

labels, and were seen on each round from 4.50 a.m. to 4.40 p.m. On the average each male was seen close enough to its label for its identity to be certain on four consecutive visits, but each female on only two visits, which shows that the females move about more than do the males. The peak of activity was less clear than in 1935, and activity lasted considerably longer, but was less intense.

The difference between the results in the 2 years is probably due to the difference in weather between the 2 days. On 15 July 1935 the temperature rose to a maximum of 27·5°, and the gall-flies had mostly vanished before 11 a.m., when the temperature (measured at 4 ft. above the ground) had risen to 24°, and the humidity was down to 51%. In 1936 the temperature only just reached 23° with an 80% humidity. The peaks of activity in both years were at almost the same temperature, near 20°, and activity had become less at 23 or 24°. This seems not to be in agreement with the experimental results at constant temperature, which showed maximum fecundity at about 30°. It may of course be that the weather conditions in which the gall-flies are most active is not near the optimum for constant conditions. Uvarov (1931) notes that the temperature preferred by an insect is greatly altered by its previous treatment; thus the ant, *Formica rufa*, prefers 23° if it has previously been at 5°, but prefers 32° if it has been at 27°. A change of similar magnitude in the gall-fly would account for the difference between the optimum in the field and the optimum under constant conditions in the laboratory.

The few gall-flies which remained in view when the temperature was at its maximum of 27° in 1935 were resting in the shade beneath leaves or flower-heads. Presumably all the gall-flies which had disappeared were hidden in the dense herbage close to the ground.

Another series of observations was made on single female gall-flies, whose activities were noted continuously, and compared with changes in the weather. Fig. 7 shows how the temperature and humidity changed during these days, and the black circles mark the times at which the flies were observed to lay eggs. Oviposition was seen over almost the whole range of conditions met, except that the lack of oviposition below 16° is probably significant. It has already been seen that in the field general activity was greatest at 20°.

The data obtained on 14 July 1936 are particularly instructive, as the weather was changing rapidly. Temperature varied between 16 and 20°. The wind was gusty, and often made it difficult to keep the gall-flies in view, owing to the movement of the plants on which they were standing. The sun shone fitfully and there were occasional showers of rain. The observations showed that neither rain nor lack of sunshine prevented oviposition, but that gall-flies were often stimulated to activity by the arrival of sunshine, and would stop moving when a cloud passed by; but this was not invariable.

Table 4

Period (G.M.T.)	Total females seen	Total males seen	Pairs	No. of females laying eggs	Temperature (°C.)	Relative humidity (%)
A. The number of gall-flies (*Urophora jaceana*) seen in an area of 60 sq.m. on 15 July 1935						
4–5 a.m.	1	0	0	0	14	83
5–6 a.m.	3	4	0	0	14	75
6–7 a.m.	3	15	0	2	15	72
7.43–8.43 a.m.	20	24	4	8	19	67
10.10–10.45 a.m.	6	6	1	1	24	51
2.30 p.m.	0	?2	0	0	24·5	50
B. The number of gall-flies seen in an area of 100 sq.m. on 7 July 1936						
4–5 a.m.	1	4	0	0	14	100
5–6 a.m.	1	8	0	0	15	100
6–7 a.m.	1	9	0	0	17·5	92
7–8 a.m.	5	15	0	0	19	81
8–9 a.m.	6	21	3	0	21	79
9–10 a.m.	6	17	3	0	21	80
10–11 a.m.	6	20	3	0	21	77
11 a.m.–1 p.m.	3	21	0	0	23	80
4–5 p.m.	3	18	0	0	19	93

(*d*) *The rate of oviposition in the field*

From these continuous observations of the gall-flies, an estimate can be made of the rate at which eggs can be deposited. The data are shown in Table 5. The eggs laid by female no. 1 were not

counted, but since the mean number of eggs laid at one time is three (p. 146) it may be surmised that about 15 eggs were laid. The rate of egg laying during the active period of this gall-fly was 16 eggs per hour. The rate for female no. 6 was 10 eggs per hour. The other flies observed laid far less rapidly, or not at all. The mean rate for all the flies on 14 July 1936 was 3 eggs per hour per female gall-fly over the whole period of observation.

If the flies maintained their maximum rate of oviposition, they would require something like 4 hr. to lay the 70 eggs which was the estimate for the fecundity in 1935, and 3 hr. to lay the 52 eggs in 1936. This is a very small proportion of the lifetime of a gall-fly, and indicates why oviposition is observed only rarely.

Although oviposition can be so rapid, and can take place over so wide a range of conditions of tempera-

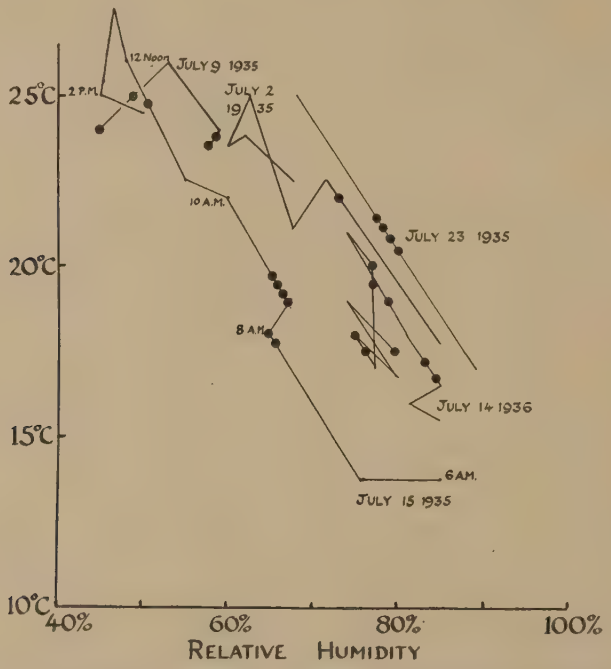

Fig. 7. Oviposition of gall-flies in relation to conditions of temperature and humidity in the field. The lines represent the changes in temperature and humidity on days when gall-flies were observed ovipositing. Black circles represent the times (B.S.T.) at which oviposition took place.

Table 5. *Observations on the behaviour of individual female gall-flies* (Urophora jaceana) *in the field*

Fly no.	Date	Period of observation (G.M.T.)	No. of flower-heads examined by fly	No. of ovipositions	No. of eggs laid	Times at which oviposition occurred
1	23 July 1935	5.50–8.25 a.m.	15	5	?	7.30, 7.40, 7.48, 8.00, 8.15 a.m.
2	14 July 1936	7.12–7.52 a.m.	3	0	0	—
3	„ „	7.39–8.25 a.m.	3	1	3	8.07 a.m.
4	„ „	8.50–11.29 a.m.	18	1	3	8.55 a.m.
5	„ „	10.45 a.m.–1.25 p.m.	6	2	5	11.23 a.m., 1.19 p.m.
6	„ „	12.14–1.16 p.m.	17	4	10	12.14, 12.30, 12.49 1.00 p.m.
7	15 July 1936	2.59–4.30 p.m.	3	0	0	—

ture and humidity, the flies in captivity contained an average of 50 apparently mature eggs when they died. Why gall-flies containing mature eggs fail to lay them remains an unanswered question.

(e) *The effect of weather on fecundity*

Oviposition was restricted in the field to the month of July, and the weather in this month was much cooler in 1936 than in 1935. This is seen in the 2-hourly means of temperature and humidity and humidity (data in Table 3), and thirdly the expectation of life at different temperatures (Fig. 6) it was calculated that the weather might be responsible for a change in the fecundity in the ratio of 1·4:1. This expected difference is not large, but it agrees with the ratio of the estimates of the fecundity in the 2 years concerned, since 70:52 = 1·3:1. However, the statistical errors in the field observations were so large that little reliance can be placed on the ratio between these figures.

To conclude, the available data are insufficient to

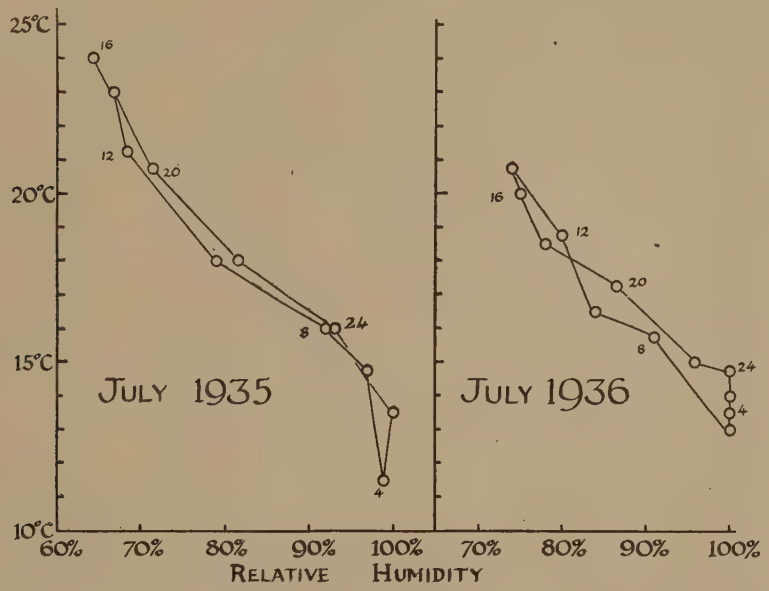

Fig. 8. Mean weather conditions for July in 1935 and 1936. Two-hourly means of temperature and humidity for the month of July in 1935 and 1936, obtained from continuous records in an out-door insectary at the Entomological Field Station, Cambridge. Numbers indicate the time of day (B.S.T.).

measurements made in an out-door insectary for the month of July in 1935 and 1936, which are plotted against each other in Fig. 8. The difference in the mean maximum temperature in the 2 years is 3°, but the humidity at corresponding temperatures was almost the same. An attempt was made to see how far this difference in mean temperature might be expected to alter the fecundity.

No rigorous method is available, and the method used is too complex and too uncertain to warrant detailed description. Using first the 2-hourly means of temperature and humidity in July 1935 and 1936 (Fig. 8), and secondly curves showing the rate of oviposition under different conditions of temperature assess the effect of weather on the fecundity of the gall-flies in the field.

PART 3

THE FACTORS WHICH AFFECT THE SURVIVAL OF THE EGGS, LARVAE AND PUPAE OF THE GALL-FLY

The mortality can conveniently be divided into two periods, the first up to the formation of the gall, and the second after this event. As the causes of the mortality and the methods of estimating it are different in the two periods, they can best be treated separately.

1. The mortality up to the formation of the gall

(*a*) *The egg mortality in* 1935

In July 1935 many eggs were found in various stages of development. In normal development the yolk first shrinks away from the ends of the egg shell, and becomes sausage-shaped. Soon the blastoderm shows as a transparent outside layer, but as differentiation proceeds to the formation of a definite larva, the blastoderm becomes less clearly distinct from the yolk within.

In 1935 49 abnormal eggs were found, which would certainly not have hatched. Of these, 12 were filled with yolk which contained large oil globules and appeared to be decaying. In 13 the yolk had shrunk from the ends of the eggs, but was still opaque, and no embryo was forming. These two types of egg were not always clearly distinct from normal eggs, but could at once be recognized if other eggs in the same batch had developed normally. In 22 eggs the yolk was irregularly shaped, twisted, or even broken into two fragments. Lastly, 2 eggs contained dead second instar larvae. All the dead eggs except the last two resembled eggs laid by unmated females; it is therefore likely that absence of fertilization prevented their development.

Few of the eggs which were alive at the time of examination would have died before hatching, and a fairly accurate estimate of the total mortality is obtainable by taking the ratio of dead eggs to the total found. The mortality was calculated only from data of egg batches in which no hatching had yet taken place. There were 148 such egg batches with a total of 447 eggs (Appendix, Table F). Of these $40/447 = 8{\cdot}9\,\%$ were dead. The standard error of this mortality is estimated to be 0·013. In only two of the egg batches which contained more than one egg were all the eggs dead.

(*b*) *The mortality of the larvae up to the formation of the gall in* 1935

The mortality in this period cannot be obtained directly, but the fact that the eggs are normally laid in groups in the flower-heads provides an indirect method by which the total mortality up to gall-formation can be estimated. The egg mortality being already known, the larval mortality can readily be found.

The frequency distribution of eggs laid is shown in Table 6, col. 2, and the same frequency distribution is given again in col. 4, but with the figures multiplied up so that the total is 886, thus making the figures comparable with the frequency distribution of gall-cells in col. 3. Had there been no mortality amongst the eggs and young larvae the frequency distribution of the gall-cells in col. 3 should have been the same as that of the eggs in col. 4, apart from sampling errors. The frequency distribution of gall-cells shows that groups 1 and 2 are larger, and groups 3–12 are smaller than in the frequency distribution of the eggs.

This difference is strongly significant, as is shown by the χ^2 test. The value of χ^2 is shown at the foot of the column, groups 7–12 having been lumped together for the purposes of its calculation, leaving seven groups. As the totals of the groups have been equalized, this leaves five degrees of freedom; Fisher's Table 3 (1934) shows that a value exceeding a tenth of this would be expected only once in a hundred trials. The strongly significant change in the frequency distribution of the gall-cells must be due to mortality in the eggs and young larvae.

The amount of this mortality can be estimated, assuming that its incidence is random, and that the death of one egg or larva in no way alters the expectation of life for other larvae in the same flower-head. Then, if there is a chance m that any one larva will die before it forms a gall, the chance that two larvae in the same flower-head will die is m^2; that only one of two will die is $2m\,(1-m)$, and the chance that neither will die is $(1-m)^2$. This reasoning can be applied to egg groups of all sizes. By multiplying the chance of mortality by the frequencies of the egg groups in col. 2 of Table 6 a new larval frequency distribution can be built up for any assumed value of random mortality. This calculation has been made for a number of different values of mortality, and for comparison with the totals found in the field the resultant frequency distributions have been multiplied by a factor to bring the sum of groups 1–12 up to 886.

These calculated frequency distributions are given in Table 6, and their goodness of fit with the observed frequency distribution of the gall-cells in col. 3 can be estimated as before from the value of χ^2, after lumping groups 7–12 together.

The values of χ^2 at the bottom of Table 6 have a minimum of 14·77, when the mortality is 0·29. The number of degrees of freedom is five, and the corresponding value of P, the probability of such a difference occurring by chance, is between 0·01 and 0·02. Such a high value of χ^2 would be expected only once in eighty trials, if the difference between the frequency distributions were due solely to random errors. This suggests strongly that the assumption of random mortality is not correct. Comparing the sums of the items in Table 6, the mortality appears to be rather higher than 0·32 for eggs in groups of four or more, and less than 0·28 for eggs laid singly or in pairs. However, the mean mortality must be near the minimum value of χ^2, which occurs when $m = 0{\cdot}289$ (Fig. 9). This figure

Table 6. *Comparison of the frequency distributions of the eggs and the gall-cells of the gall-fly* (Urophora jaceana) *in* 1935

Frequency of flower-heads containing each number of eggs or gall-cells

No. of eggs or gall-cells	Observed frequency		Calculated frequency of flower-heads with gall-cells if random mortality = m										
	Eggs	Gall-cells	$m=0$	$m=0.2$	$m=0.25$	$m=0.26$	$m=0.27$	$m=0.28$	$m=0.29$	$m=0.30$	$m=0.31$	$m=0.32$	$m=0.35$
0	—	.	—	48·28	66·18	70·15	74·26	78·52	82·93	87·50	92·23	97·16	113·09
1	29	287	173·61	249·13	272·06	276·85	281·70	286·62	291·61	296·66	301·79	306·98	322·98
2	38	272	227·48	266·32	272·46	273·48	274·43	275·30	276·10	276·83	277·49	278·06	279·33
3	36	196	215·51	189·79	180·16	178·14	176·09	174·01	171·91	169·78	167·64	165·47	158·81
4	23	79	137·69	92·22	83·66	82·04	80·43	78·84	77·27	75·75	74·19	72·66	68·16
5	8	29	47·89	39·94	37·18	36·56	35·93	35·27	34·60	33·90	33·20	32·47	30·21
6	5	20	29·93	24·77	21·51	20·84	20·17	19·50	18·84	18·17	17·51	16·87	14·97
7	5	2	29·93	13·10	10·33	9·84	9·38	8·93	8·51	8·11	7·72	7·35	6·34
8	2	0	11·97	4·86	3·98	3·84	3·69	3·56	3·43	3·30	3·18	3·06	2·71
9	1	1	5·99	2·34	2·14	2·09	2·04	1·98	1·91	1·84	1·77	1·70	1·46
10	0	0	0	1·79	1·49	1·42	1·34	1·26	1·18	1·10	1·02	0·95	0·73
11	0	0	0	1·30	0·82	0·73	0·66	0·59	0·53	0·47	0·42	0·37	0·25
12	1	0	5·99	0·43	0·20	0·17	0·15	0·13	0·11	0·09	0·08	0·06	0·04
Total 1–12	148	886	886·0	886·0	886·0	886·0	886·0	886·0	886·0	886·0	886·0	886·0	886·0
χ^2, lumping groups 7–12			168·35	30·22	17·84	16·47	15·52	14·91	14·77	14·99	15·63	16·73	22·65

Table 7. *Comparison of the frequency distributions of the eggs and the gall-cells of the gall-fly* (Urophora jaceana) *in* 1936

Frequency of flower-heads containing each number of eggs or gall-cells

No. of eggs or gall-cells	Observed frequency		Calculated frequency of flower-heads with gall-cells if random mortality = m									
	Eggs	Gall-cells	$m=0$	$m=0.2$	$m=0.25$	$m=0.27$	$m=0.29$	$m=0.30$	$m=0.31$	$m=0.32$	$m=0.33$	$m=0.34$	$m=0.35$
0	—	—	—	18·47	24·82	27·64	30·63	32·20	33·82	35·50	37·23	39·02	40·87
1	22	90	72·25	88·88	94·36	96·72	99·18	100·45	101·75	103·08	104·43	105·79	107·22
2	18	96	59·11	72·28	75·12	76·19	77·23	77·73	78·22	78·70	79·16	79·64	80·05
3	18	57	59·11	56·41	55·56	55·14	54·66	54·40	54·12	53·82	53·50	53·16	52·81
4	11	26	36·12	35·03	33·44	32·66	31·79	31·32	30·84	30·34	29·82	29·29	28·73
5	9	10	29·56	21·66	18·98	17·89	16·80	16·25	15·71	15·17	14·63	14·08	13·57
6	6	4	19·70	9·96	7·97	7·25	6·58	6·26	5·94	5·64	5·35	5·06	4·79
7	3	5	9·85	3·25	2·50	2·24	1·99	1·88	1·76	1·66	1·56	1·45	1·36
8	0	0	0	1·06	0·80	0·71	0·61	0·57	0·53	0·49	0·45	0·41	0·38
9	1	1	3·28	0·47	0·27	0·21	0·17	0·15	0·13	0·11	0·10	0·09	0·08
Total 1–9	88	289	289·0	289·0	289·0	289·0	289·0	289·0	289·0	289·0	289·0	289·0	289·0
χ^2, lumping groups 6–9			59·11	17·93	12·15	10·53	9·36	8·96	8·71	8·59	8·63	8·82	9·21

has been used in calculations in other parts of this paper.

It is necessary to estimate the standard error of the χ^2 minimum to find the accuracy of the estimate of the mortality. I am indebted to Prof. R. A. Fisher for the method employed. The variance of a

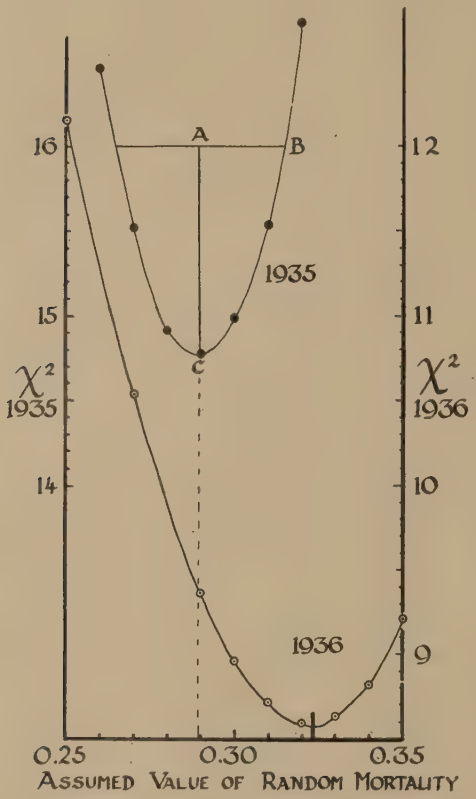

Fig. 9. Estimation of random mortality from χ^2 minimum. The values of χ^2 in Tables 6 and 7 are plotted against the values assumed for the random mortality. The construction on the curve indicates the method used for estimating the standard error of the χ^2 minimum, see text.

χ^2 minimum equals twice the radius of curvature of the χ^2 curve at the minimum. The curve is shown in Fig. 9, and the radius is measured by $AB^2/2AC$, since the curve is parabolic. The standard error so estimated was found to be 0·022.

To conclude this section, the larval mortality prior to gall-formation is obtained by subtracting the mortality in the egg stage (0·089) from the total mortality (0·289). This leaves a larval mortality of 0·20, expressed as a fraction of the eggs laid. Expressed in terms of the larvae which hatched it becomes 22%.

For the most part this larval mortality was not directly observed, and much of it may have been due to intrinsic causes which killed the larvae before they formed galls in the florets. However, in a single instance two larvae were found in the same floret, and one of them was already dead. This observation suggests that some of the larval mortality was due to competition, and provides an explanation for the fact that the mortality seemed to be higher in the large egg batches than in the small.

The early larval mortality is therefore to be regarded as density dependent, and its operation will be considered in more detail in the discussion.

(*c*) *The egg mortality in* 1936

Eggs were found in 1936 from the beginning of July to the middle of August. In the 88 egg batches found in which no hatching had yet taken place, there were in all 267 eggs of which 41 were dead (Appendix, Table G). The egg mortality was therefore 15·3%, with an estimated standard error of 0·022.

Altogether 49 dead eggs were examined in 1936. Of these 21 were filled with decaying yolk, 7 had the yolk contorted, the yolks of 17 were opaque and stumpy, and 4 larvae had died in the first instar while still within the egg. The proportions of the different types of dead eggs were rather different than in 1935. Moreover, in 1936 about half of the dead eggs were found in egg batches in which every egg was undeveloped and dead. These dead eggs resembled those laid by unmated females. It may be inferred that the low population density of gall-flies in 1936, which led to interspecific mating in a number of instances, also led to the laying of eggs by unmated or cross-mated females.

(*d*) *The mortality of the larvae up to the formation of the gall in* 1936

Table 7 shows the frequency distribution of the eggs laid and of the gall-cells discovered in 1936, and in cols. 4–10 are shown the frequency distributions derived from the egg distribution assuming different values for random mortality. These expected distributions are compared with the frequency distributions of gall-cells in col. 3 by the χ^2 test, having lumped groups 6–9 together, leaving four degrees of freedom. The values of χ^2 are plotted in Fig. 9. The minimum value of P is between 0·1 and 0·05. This value is not unreasonably high, and the figures are not inconsistent with the assumption that the difference between the frequency distributions of eggs and gall-cells was due to random mortality. As

already noted, in 1935 the data suggested that the mortality was not random. The difference between the results in the 2 years cannot be attributed to a greater degree of competition in 1935, since the mean number of larvae in the occupied flower-heads, and hence the competition, was very slightly greater in 1936 than in 1935. Possibly the smaller amount of data available for 1936 is insufficient to demonstrate the effect observed in 1935, owing to the concomitant reduction in accuracy.

The random mortality occurring between the laying of the eggs and the formation of the galls is estimated from the χ^2 minimum to be 0·323. The standard error of the estimate, determined from the graph, is 0·035. This mortality includes only a part of the egg mortality. Half of the 15·3 % egg mortality was of entire egg batches, which would not alter the frequency distribution of the gall-cells, so long as small and large batches failed to hatch with equal frequency. Only the remaining 7·6 % of the egg mortality was probably random, and would be included in the 32·3 % total random mortality up to gall-formation. This leaves

$$0{\cdot}323\ (100-7{\cdot}7)-7{\cdot}6=22{\cdot}2\ \%$$

as the random mortality of the larvae or

$$\frac{22{\cdot}2}{(100-15{\cdot}3)}=26{\cdot}2\ \%$$

when expressed in terms of the larvae which hatched.

The over-all mortality from the egg stage up to the formation of the gall consisted of $7{\cdot}7\pm2{\cdot}2\ \%$ mortality of whole egg batches followed by $32{\cdot}3\pm3{\cdot}5\ \%$ random mortality of the remainder, which taken together give an over-all mortality of $37{\cdot}5\pm3{\cdot}4\ \%$.

The relation between these various figures is made clearer by the following schematic representation:

				Nos. left from each 100 eggs laid	Mortality given as successive percentages
Dead eggs 15·3 %	7·7 %	whole batches		7·7 dead eggs	7·7
	7·6 %	random		7·6 dead eggs	8·2
Live eggs 84·7 %	Total random death of eggs and larvae		32·3 %	22·2 dead larvae	26·2
	Survival		67·7 %	62·5 live larvae	
100·0 %			100·0 %	100·0 %	

2. The mortality after the formation of the gall

The examination of square-metre samples of knapweed throughout the summer gave information about the contents of each gall-cell. From these data, with the addition of those already given in the previous sections, it has been possible to build up a picture of the course of events over the period of 2 years.

The following method was used. The totals for ten or more successively collected square-metre samples were added together, and the mean numbers or percentages of gall-fly larvae killed by various agencies were found. The census data also gave the period of time over which each agency operated, and the results were built up into Table 8, which shows both the time of operation and the numerical effect of every important factor.

For those factors which operated simultaneously separate percentages are not given. Similar tables are given by Schwerdtfeger (1936) for the mortality of the moth *Dendrolimus pini*, which is a serious pest of conifers in north Germany.

The census of galls on the standing stems of knapweed began in February 1935, but the first complete census including fallen galls was not made until May. However, although the fallen galls were omitted, the census of 10 sq.m. in February 1935 gave an idea of the factors which had caused mortality in the previous summer. But they provided a low estimate of the total numbers.

In the sections which follow, each of the major causes of mortality listed in Table 8 will be given separate consideration.

(*a*) *Winter disappearance*

The total number of newly formed gall-cells found in the late summer of 1935 was estimated from twenty samples to be $147{\cdot}6\pm21{\cdot}5$ per sq.m. (Appendix, Table A). By the following spring and early summer the mean for 36 sq.m. had fallen to $56{\cdot}8\pm7{\cdot}0$ gall-cells per sq.m. (Appendix, Table C). This difference is strongly significant, and the winter disappearance was estimated to be $61{\cdot}5\pm7{\cdot}3\ \%$.

That this loss was due in part to the observer's failure to notice the galls is certain, but in some at least of the sq.m. samples examined this explanation is quite inadequate. Some of the sq.m. were crossed by a maze of mouse or vole runs, and when the vegetation was cleared away the soil surface was almost smooth. It is inconceivable that under these conditions more than 5 % of the fallen galls could have been overlooked. Yet it was in these places that fewest galls were found. Frequently small piles of partly destroyed galls were found in mouse runs, and

Table 8. *The effect of successive mortality factors on the numbers of the knapweed gall-fly* (Urophora jaceana) *found per sq.m. at Madingley*

Non-specific mortality (i.e. that which affects the gall-fly and its parasites indiscriminately) is marked with an asterisk.

			% killed	No. killed per sq.m.	No. alive per sq.m.
1934	July	No. of larvae in gall-cells	—	—	43 larvae
		Died due to unknown causes	5	2	41 ,,
		Parasitized by *Eurytoma curta*	15	6	35 ,,
	Aug.	Miscellaneous parasitism:			
		Habrocytus trypetae	39	4	—
		**Torymus cyanimus*		3	—
		**Tetrastichus* sp.		2	—
		*Destroyed by caterpillars		4·6	21·4 larvae
1935	Winter	*Winter disappearance not estimated	?	?	21·4 ,,
		*Destroyed by mice	18·5	4	17·4 ,,
	May–June	Miscellaneous parasitism:			
		Habrocytus trypetae	60	10	—
		**Macroneura vesicularis*		0·4	—
		**Tetrastichus* sp.		0·1	6·9 flies
	July	6·9 flies emerged per sq.m., 42½% were females			
		Mean number of eggs laid: 70 per female	—	—	203 eggs
		Infertile eggs	9	18·3	184·7 ,,
		Larvae died before forming galls	20	37·1	147·6 larvae
		Larvae died in galls due to unknown cause	2	3	144·6 ,,
		Parasitized successfully by *Eurytoma curta*	45·5	65·8	78·8 ,,
	Aug.–Sept.	Miscellaneous parasitism:			
		Habrocytus trypetae	37	5·6	—
		**Eurytoma robusta*		4·1	—
		**Torymus cyanimus*		3·7	—
		**Tetrastichus* sp.		0·6	—
		*Destroyed by caterpillars		14·8	50 larvae
1936	Winter	*Winter disappearance	61·5	30·8	19·2 ,,
		*Destroyed by mice	64	12·2	7·0 ,,
		Larvae died due to unknown causes	26	1·8	5·2 ,,
	May–June	Miscellaneous causes:			
		*Birds	31	0·4	—
		Habrocytus trypetae		0·7	—
		**Macroneura vesicularis*		0·25	—
		**Tetrastichus* sp.		0·25	3·6 larvae
	July	*Drowned in floods	44	1·57	2·03 flies
	July	2·03 flies emerged per sq.m., 42½% were females			
		Mean number of eggs laid: 52 per female	—	—	44·8 eggs
		Infertile eggs	15·3	6·9	37·9 ,,
		Larvae died before forming galls	26·2	9·9	28·0 larvae
		Larvae died in galls due to unknown causes	4·3	1·2	26·8 ,,
		Parasitized by *Eurytoma curta*	27	7·2	19·6 ,,
	Aug.–Sept.	Miscellaneous parasitism:			
		Habrocytus trypetae	36	0·2	—
		**Eurytoma robusta*		1·6	—
		**Torymus cyanimus*		1·5	—
		**Tetrastichus* sp.		0·2	—
		Killed by *Lestodiplosis*		0·2	—
		*Destroyed by caterpillars		3·3	12·6 larvae

much of the winter disappearance was probably due to mice carrying galls underground.

For this reason the 61·5% winter disappearance has been counted as a form of mortality in the calculations which follow.

As a summer census was not made in 1934 it is not possible to estimate the winter disappearance for 1934–5. In the first census, made in February 1935, the mean number of gall-cells found on the standing stems was 43 ± 9, by which time, of course, an unknown number of galls had already fallen. By July 1935 a mean number of only 15 gall-cells remained on the standing stems in each sq.m., but a mean of 23 per sq.m. was found fallen to the ground. This gives a mean total of 38 ± 10 gall-cells per sq.m., which is not significantly less than the 43 ± 9 found in February. Probably winter disappearance was much less than in the following winter. As the winter disappearance is believed to be due to mice, it is also significant that mouse damage was far less also (Table 8).

(*b*) *Mortality due to mice*

Many of those galls which fell to the ground during the winter became quite free from the flower-heads in which they were formed. At the base of some of them were large gaping holes, each opening into a separate gall-cell. Sometimes the whole wall of the gall was destroyed, leaving perhaps only one partly intact gall-cell. Such gall-cells never contained any live insect larva or pupa, and their previous history could not be inferred unless perhaps fragments of a puparium of the gall-fly indicated previous attack by the chalcid parasite *Eurytoma curta*.

The evidence that mice destroyed these galls is as follows: Only the fallen galls were affected. They were often found in small heaps in mouse runs. The holes in the galls had been made from the outside, and were not at all like the neat circular holes made by emerging parasitic Hymenoptera. The galls were attacked with great thoroughness, and usually had a hole into each gall-cell. It was only in the largest galls, with six or more cells, that the central cell was sometimes intact. Whatever did the damage must have turned the gall over to deal with it from all sides. It is extremely unlikely that any insect would do this, and the only other likely animals are mice, voles or shrews. There is no direct evidence available, but in view of the facts put forward it is concluded that mice or voles were responsible.

The percentage of gall-cells found destroyed by mice was 18·5% early in 1935 and 64% early in 1936. As mice were probably responsible for most of the 61·5% winter disappearance in 1935–6, mice may have caused a mortality of 86% of the gall-fly larvae in the gall-cells of the 1935–6 generation.

As already noted, mice attacked only the fallen galls. In June and July 1935 the total number of gall-cells per sq.m. was 38, of which 23 had fallen. Of the latter 6·5, or 28%, were destroyed by mice. In 1936 the total number of gall-cells was 57 per sq.m., and 53 of these had fallen, of which 36, or 68%, had been destroyed by mice.

(*c*) *Mortality due to unknown causes*

A proportion of the larvae and pupae of the gall-fly were found dead or destroyed without the cause being apparent. Into this class will fall all the mortality which is not due to parasitic and predaceous insects, or to mice. It will therefore include any mortality due to parasitic disease, roving predators (e.g. mites), fungi, and climatic factors, as well as any intrinsic functional failure. The appearance of the dead larvae varied greatly. In a few cases the gall-cell was empty, and there was no sign that the soft tissues of the gall had been eaten; these larvae must have died at a very early stage. Some dead larvae were brown and flabby, while others were dry and hard, and covered with fungal hyphae. Dr Petch very kindly named the fungi as *Aegerita* sp., *Fusarium* sp., *Cladosporium* sp. and *Cephalosporium muscarium*. None of these is a parasitic species, and it is very likely that they attacked the fly larvae only after death.

There is no evidence that climatic factors prove fatal in winter. Nor is high temperature in summer ever likely to be lethal to the larvae under natural conditions in England. Experiment showed that for 1 hr. exposure the upper fatal limit of the larvae was about 43° C. The temperature of the inside of a flower-head in bright sunshine did not exceed that of the air by more than 5°, as was shown by measurements made with a small thermocouple. The larvae would be subjected to a temperature of 43° only if the air temperature reached or exceeded 38°, which is 10° higher than any reading taken during the period of the census.

The gall-fly larvae are very resistant to dry conditions, and when fully grown they can be kept for months in dry gelatine capsules, in which they will complete their development, and emerge as flies. Gelatine capsules are in general rapidly fatal to most fly larvae, unless the humidity is kept very high. Equally the wet conditions of the winter seem to cause little or no mortality to the gall-fly larvae in the field.

The only evidence that climatic factors caused the death of any of the inhabitants of the galls was seen in the very wet period in July 1936, when the ground was waterlogged and covered with puddles for some days. Such conditions were fatal to a large proportion of the larvae and pupae of the gall-fly and its parasites which were submerged in the fallen galls.

Some of the mortality included in unknown causes may be due to the feeding habits of the chalcid parasite, *Habrocytus trypetae*. The females of this parasite sometimes fed on larvae in the gall without laying eggs, and, unless the delicate feeding tube was found, the cause of destruction would not be apparent.

(*d*) *Mortality due to chalcid parasites*

The gall-fly larvae and pupae in the puparia were attacked by parasites at three main periods in the year. Some of the common species are illustrated in Fig. 10. The common *Eurytoma curta* laid its eggs in the gall-fly larvae soon after they had hatched, and the parasites destroyed their hosts soon after the latter had completed their growth in August.

From the time when the gall-fly larvae approached full size until the end of the summer, they were attacked by various other chalcids, chief amongst which were *Torymus cyanimus*, *Eurytoma robusta*, *Habrocytus trypetae*, and *Tetrastichus* sp. B, all except the last of which are ectophagous.

The third period of attack began in the early summer of the following year, when other generations of *Habrocytus trypetae* and *Tetrastichus* sp. B, and *Macroneura vesicularis* attacked any larvae or pupae of the gall-fly or of any other parasite which was in the galls. The competition between the various species was severe. The method of attack of each species is described below, and the hosts selected for attack and the success of the attacks are considered.

In one or two instances gall-fly larvae were found which had apparently been killed by the very small larvae of the predacious gall-midge *Lestodiplosis miki*. These larvae normally attacked other gall-midge larvae present in the flower-heads. They have been described by Otter (1938).

(1) *Eurytoma curta* (Fig. 10A)

Eurytoma curta parasitizes only the larvae of the gall-fly *Urophora jaceana* in the knapweed, but it has been recorded as a parasite of various gall-forming insects on other plants, such as the gall-flies *Urophora eriolepidis* (Lw.), *U. stylata* (Fabr.), *U. cardui* (L.), *Tephritis vespertina* (Lw.) and the gall-wasp *Aulacidia hieracii* (Bouché). No other trypetids were common on the site of the census breeding in plants other than the knapweed, although a few specimens of *Urophora stylata*, *Xyphosia miliaria* (Schr.) and *Icterica westermanni* (Meig.) were seen. No evidence was obtained to indicate whether or not these were attacked, but they were far too uncommon to be important alternative hosts.

The adults of *Eurytoma curta* emerge mostly in the first half of July. Out of 103 adults reared fifty-four were females, which gives a proportion of $0{\cdot}52 \pm 0{\cdot}05$ females. The details of the search for hosts and the spatial distribution of parasitism have been described elsewhere (Varley, 1941). The females discover flower-heads of the knapweed during flight, and often alight and walk over them, tapping them with the antennae. They may eventually insert the ovipositor into a flower-head, even though, as shown by subsequent dissection of the flower-head, it may be devoid of hosts. The gall-fly larvae are suitable for attack soon after hatching from the egg (in the second instar), but no eggs have been found in third instar gall-fly larvae.

An individual gall-fly larva spends about 2 weeks in the second instar. In 1935 second instar larvae were found between 9 July and 25 August, and females of *Eurytoma curta* were seen in the field between 9 July and 6 August. In 1936 the hosts were available from 17 July to 1 September, and the females of *E. curta* were seen in the field between 7 July and 8 August. The census showed that some *E. curta* must have emerged later than this, for some pupae of *E. curta* collected from fallen galls in August did not emerge in captivity until early September, when there were no suitable hosts in the knapweed. The retarded emergence of these individuals was probably one of the effects of flooding.

Probably in normal years the emergence of *E. curta* corresponds fairly closely with the period during which gall-fly larvae are suitable for parasitization.

The egg and larval stages have been described elsewhere (Varley, 1937*a*). The egg is like a short sausage with a long 'tail', and its volume may be as much as a tenth of that of the host in which it is laid. The egg hatches in a few days, but the endophagous larva grows very slowly, and is usually in the third instar when the gall-fly larva is fully grown in August. At this time the parasite exerts a peculiar influence on the host, which, instead of passing into a diapause and hibernating in the larval state, turns to face the exit of the gall-cell, and forms its puparium (Varley & Butler, 1933). Inside the brown puparium of the host the parasite larva begins to grow rapidly, and consumes its host completely within a few days. It passes the winter as a fifth instar larva in the otherwise empty puparium of the host. This early pupation makes it very easy to recognize parasitized hosts, until the normal time for pupation comes in May (Fig. 3G).

The number of *E. curta* per sq.m. during the period of the census is indicated in Table 9. The factors which caused mortality were mostly the same as for its host, the gall-fly, and the percentages killed by mice, and winter disappearance, have been given the same values as for the gall-fly in Table 8, since these factors destroyed the contents of the gall more or less indiscriminately.

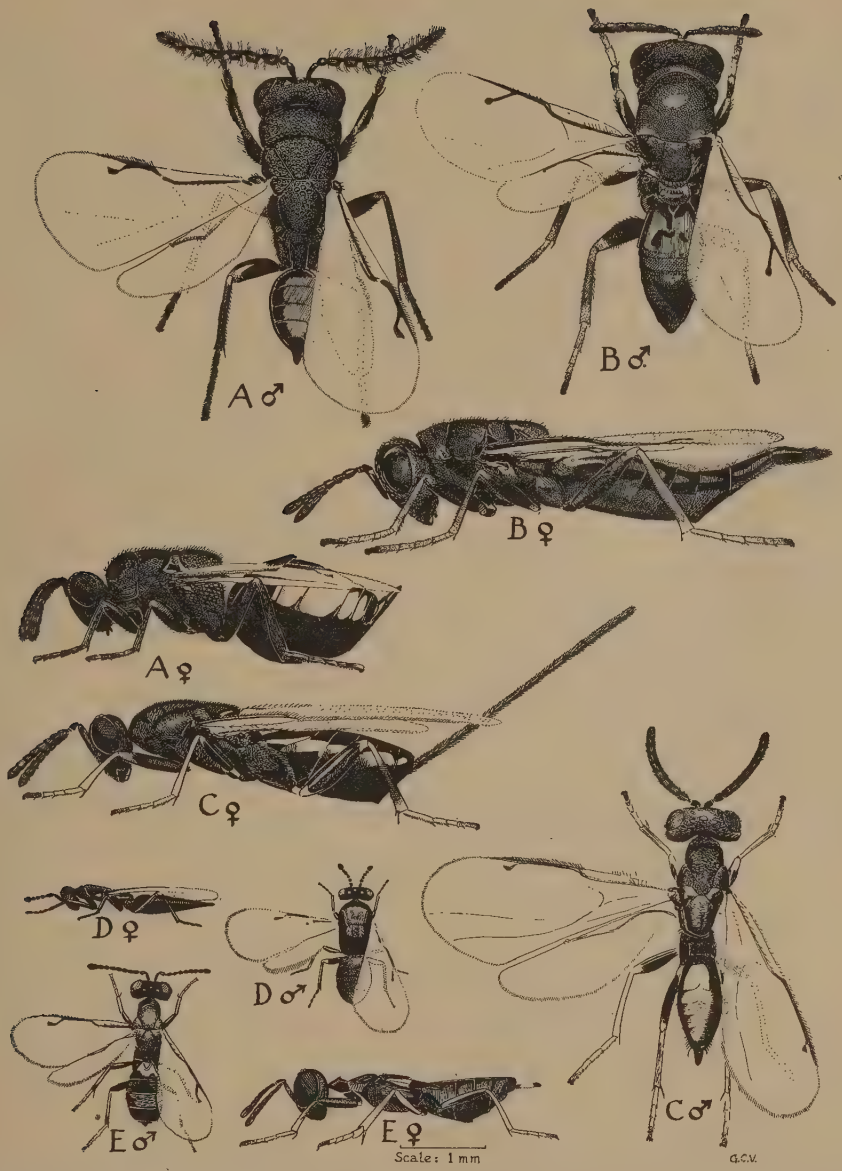

Fig. 10. Chalcid parasites of the knapweed gall-fly. A. *Eurytoma curta*: colour black except for brown fore-tibiae, brown apices of the femora, and brown tarsi. (*E. robusta* differs mainly in the shape of the abdomen.) B. *Habrocytus trypetae*: colour of head thorax and abdomen dark metallic green; coxae and all but apices of femora metallic green; tibiae and apices of femora brown, tibiae centrally infuscate; tarsi yellow, last joint dark brown. C. *Torymus cyanimus*: colour brilliant metallic green with blue and violet reflexions; legs mainly bright yellow, but femora centrally and coxae wholly metallic green, and hind tibiae centrally infuscate. D. *Tetrastichus* sp. B: colour dull metallic green, legs brown. E. *Macroneura vesicularis*: colour very dull green with dull coppery reflexions. Legs of female pale yellow with darkened femora. Legs of male with dark apices to hind and mid tibiae.

The mortality due to parasitism in August and September is inevitably rather too low in Table 9. As will be seen later, the ectoparasites do not (with the exception of *Habrocytus trypetae*) choose between healthy larvae of the gall-fly, and those which already contain larvae of *Eurytoma curta*. Cases of multi-parasitism were observable only before the host was completely consumed by an ectoparasite. Many found later than this doubtless escaped notice, and other parasites had hatched, then the newly hatched ectophagous larvae died of starvation, being unable to bite through the hard puparium; and the *E. curta* survived. The acceleration of the host's pupation by *E. curta* is thus advantageous to the parasite, as it protects it from the attacks of some of its enemies.

Those ectophagous chalcids which attacked after *E. curta* had completed the destruction of the gall-fly within its puparium sometimes laid their eggs

Table 9. *The effect of successive mortality factors on the numbers of the chalcid parasite* Eurytoma curta *found per sq.m. at Madingley*

Non-specific mortality (i.e. that which affects the gall-fly and its parasites indiscriminately) is marked with an asterisk.

			% killed	No. killed per sq.m.	No. alive per sq.m.
1935	Feb.	Larvae per sq.m.	—	—	2·7 larvae
	May–June	Miscellaneous parasitism:			
		Habrocytus trypetae	26	0·4	—
		*Other parasites		0·3	2·0 adults
	July	2·0 adults emerged per sq.m., 52 % were females			
		Mean number of eggs laid: 63 per female	—	—	66 eggs
		Egg or larva died—host survived	0·3	0·2	65·8 larvae
	Aug.–Sept.	Miscellaneous parasitism:			
		**Torymus cyanimus*		0·2	—
		Habrocytus trypetae		0·6	—
		**Tetrastichus* sp.	25	0·4	—
		Died due to unknown causes		0·5	—
		*Destroyed by caterpillars		14·1	50 larvae
1936	Winter	*Winter disappearance	61·5	30·8	19·2 ,,
		*Destroyed by mice	64	12·3	6·9 ,,
		Missing	33	2·3	4·6 ,,
		*Destroyed by birds		0·4	—
	June	Miscellaneous parasitism:			
		Habrocytus trypetae	26	0·3	—
		**Tetrastichus* sp.		0·3	—
		**Macroneura vesicularis*		0·1	3·5 larvae
	July	*Drowned in floods	53	1·84	1·66 adults
	July	1·66 adults emerged per sq.m., 52 % were females			
		Mean number of eggs laid: 8·4 per female	—	—	7·2 eggs
	Aug.–Sept.	*Miscellaneous parasitism		0·3	—
		Died due to unknown causes	25	0·1	—
		*Destroyed by caterpillars		1·4	5·4 larvae

the death of the gall-fly would be credited solely to the successful ectoparasite. The incidental death of any small *Eurytoma* larva would be unrecorded.

Although the ectophagous larvae of the chalcids *Torymus cyanimus*, *Habrocytus trypetae* and *Macroneura vesicularis* might destroy the larva of *Eurytoma curta* with that of its host, the outcome of such competition depended very much on the circumstances, and in particular on the timing of the attack. If the *E. curta* larva had caused the pupation of the gall-fly larva to begin before the eggs of the uselessly outside the puparium, and sometimes laid them within the puparium on the body of the larva of *E. curta*, which then served as a host. Only those *E. curta* remaining in the standing flower-heads were subject to this form of attack, which was prevalent in the spring.

Three instances were noted in which a healthy gall-fly larva contained a dead egg of *E. curta*. Two other gall-fly larvae contained either a dead egg or larva of *E. curta*, but both had also been attacked by *E. robusta*, which may perhaps have been responsible

for the death of the *E. curta* larva. These instances have been included in Table 9 in the 0·3 % mortality in July 1935.

Six cases were observed in August and September in which either a dead gall-fly larva or dead gall-fly puparium contained a dead larva of *E. curta*. These have been included in the 0·5 *E. curta* found per sq.m. to have died from unknown causes.

One case of superparasitism was observed. Two larvae of *E. curta*, one of them already dead, were found in a single live host.

The mortality of *E. curta* in the winter of 1935–6 requires further explanation. Starting from the calculated number of eggs per sq.m., the expected number of live *E. curta* at the end of 1935 was 50 per sq.m. (Table 9). But in the census in September a mean of only 46 was found. In the following spring the number found alive, recently killed, or parasitized was only 4·6 per sq.m., instead of the expected figure 6·9. This latter figure is based on the values of destruction by mice and winter disappearance, assuming these factors to have acted equally on both *E. curta* and gall-fly larvae. The difference (2·3) between these figures is recorded as 'missing' in Table 9. It may easily be due to random sampling errors, as the two figures are based on different samples.

Of the remaining 4·6 *E. curta* larvae found per sq.m. in June, 0·4 in the galls in the standing flower-heads had been destroyed from the outside, presumably by birds (tits, *Parus* spp. have been seen feeding on knapweed galls) and 0·7 per sq.m. suffered parasitism by various chalcids, leaving 3·5 per sq.m. Of this remainder 53 % were drowned by the July floods, leaving a mean number of only 1·66 adult *E. curta* to emerge per sq.m.

The fecundity of *E. curta* is shown in Table 9 for the two generations studied. Details of the computations are given in the Appendix, Tables D and E. The values are subject to large sampling errors because of the small number of adults which emerged per sq.m. In July 1935 $2{\cdot}00 \pm 0{\cdot}65$ adults emerged per sq.m., and the number of eggs laid per female was estimated to be 63 ± 23. In 1936 $1{\cdot}66 \pm 0{\cdot}38$ adults emerged per sq.m., and the number of eggs laid was estimated to be only $8{\cdot}3 \pm 2{\cdot}6$ per female. Although the standard errors of the estimates are large, the seven-fold difference between the mean number of eggs laid in the 2 years is significant ($P < 0{\cdot}05$).*

* The difference between the estimates of the fecundity in the 2 years $(63 \pm 23) - (8{\cdot}3 \pm 2{\cdot}6) = 54{\cdot}6 \pm 23{\cdot}2$. The probability of this difference arising by chance can be estimated by the t test, where $t = 54{\cdot}6/23{\cdot}2 = 2{\cdot}36$.

The standard error of the difference is almost the same as that of the larger estimate of the fecundity, which was itself derived from the data

This reduction in the fecundity of *E. curta* in 1936 must be partly due to the cold weather. Now the gall-fly's oviposition period overlapped with that of *E. curta*, and the two species might be expected to have been similarly affected. But whereas the fecundity of the gall-fly fell from 70 to 52 eggs per female, that of *E. curta* fell from 63 to 8·4. The change is far greater than can be accounted for by the weather.

The only other factor likely to have affected the fecundity of *E. curta* is the availability of hosts. Table A in the Appendix shows that in 1935 there were 147·6 gall-fly larvae distributed amongst 240 flower-heads per sq.m., giving a mean of 0·61 suitable hosts per flower-head. For 1936 Table B in the Appendix shows that there were only 28 gall-fly larvae in 140 flower-heads, giving a mean of 0·2 hosts per flower-head. Thus the host population density expressed as gall-fly larvae per flower-head is only one-third as great in 1936 as in the previous year. *E. curta* seeks its hosts by probing with the ovipositor, and probes flower-heads either with or without any contained hosts. Hence, other conditions being equal, the rate of discovery of hosts would be expected to be about a third as great in 1936 as in 1935.

The estimated fall in the fecundity of *E. curta* is not significantly bigger than the combined effect of these two factors, of which the most important is the fall in host density. This result supports the view that the difficulty in finding hosts was the main factor limiting the mean number of eggs laid per female of *E. curta*. The great reduction in the success of searching in 1936 apparently caused no substantial increase in the number of flower-heads examined by each female.

Since the reproductive rate of the parasite *E. curta* appears to be controlled by host density, this parasite is presumed to act on the gall-fly as a delayed density dependent factor. This relationship is further considered in the discussion.

(2) *Eurytoma robusta*

The adults of this species resemble those of *E. curta* very closely, but the female has a rather longer abdomen. However, the larvae of *E. robusta* are ectophagous, and both eggs and larvae are easily distinguished from those of the other species. The dark brown eggs are laid on the third instar larvae

$$\frac{(144{\cdot}6 \pm 21{\cdot}5)\,(0{\cdot}457 \pm 0{\cdot}010)}{(2{\cdot}0 \pm 0{\cdot}65)\,(0{\cdot}52 \pm 0{\cdot}05)}$$

in which by far the largest contribution to the standard error is made by the figure $2{\cdot}0 \pm 0{\cdot}65$, which is based on a sample of thirteen items, with twelve degrees of freedom.

With twelve degrees of freedom a value of $t = 2{\cdot}18$ corresponds to a probability $P = 0{\cdot}05$.

of the gall-fly in August, and the parasite larvae feed singly and rapidly destroy the hosts. They then feed a little on the gall-tissue, and leave a number of small woody chips in the gall-cell (larvae of the related genus *Harmolita* are entirely photophagous). The winter is passed in the larval stage and the adults emerge in the following July and August. This species has been recorded as a parasite of the thistle gall-fly *Urophora cardui* L., and of the gall-wasp *Aylax papaveris* (Perris), and has been reared from the flower-heads of various species of *Centaurea* and from *Carduus crispus* L.

The distribution of this species in space was very irregular (Varley, 1941). No trace of it was discovered in the preliminary census work in thirty-six different localities in England and Wales. In the census area it was first found in the fresh flower-heads in July 1935, when a few eggs and young larvae were seen. Its distribution in the various sq.m. samples was also very patchy. 23 sq.m. were examined during the time when this species was available for discovery, and over half of the 83 hosts found attacked were discovered in 3 adjacent sq.m. In 1936 its localization was even greater, and 32 out of 38 parasitized hosts were in a single one of the 20 sq.m. samples examined.

Table 10 shows the changes in the numbers of live *Eurytoma robusta* found per sq.m.

In a number of instances two or more eggs of *E. robusta* were found in a single gall-cell of the host, although only one parasite at most could mature on the one host. Such superparasitism has been discussed elsewhere (Varley, 1941). It accounted for 6·7 % of the mortality in 1935 and 28 % in 1936. A smaller percentage of larvae failed to kill the gall-fly larvae and died themselves. In the summer of 1935 a few larvae of *E. robusta* were found parasitized by the chalcids *Habrocytus trypetae* and *Tetrastichus*. In August 1936 25 % of the larvae of *Eurytoma robusta* hatched from eggs laid on such tiny gall-fly larvae that they were only half grown when the host was completely consumed. Their food supply exhausted, they died of starvation.

There is some information about host selection. The female parasites which emerged in August 1936 sought their hosts at a time when many were still very small. As noted above, these small gall-fly larvae were accepted as hosts, although they were unsuitable for the parasite larvae. In seven out of twenty-one instances it was possible to see that the gall-fly larva had previously been parasitized by *E. curta*. This indicates that parasitized and unparasitized hosts were accepted by *E. robusta* with approximately equal readiness. The endophagous larva of *E. curta* was always killed when its host was parasitized and killed by the ectophagous larva of *E. robusta*.

Table 10. *The effect of successive mortality factors on the numbers of the chalcid parasite* Eurytoma robusta *found per sq.m. at Madingley*

			% killed	No. killed per sq.m.	No. alive per sq.m.
1935	July	No. of eggs	—	—	4·5 eggs
		Died due to superparasitism	6·7	0·3	4·2 larvae
		Failed to attack host	3	0·12	4·08 ,,
	Aug.	Miscellaneous causes:			
		Parasitism		0·12	—
		Destroyed by caterpillars	7	0·06	—
		Died due to unknown causes		0·12	3·78 larvae
1936	Winter	Winter disappearance	61·5	2·33	1·45 ,,
		Destroyed by mice	64	0·93	0·52 ,,
	July	Died due to unknown causes Drowned in floods	80	0·42	0·10 adults
	July	0·1 adults emerged per sq.m., 50 % were females			
		Mean number of eggs laid: 50 per female	—	—	2·5 eggs
		Died due to superparasitism	28	0·7	1·8 larvae
		Failed to attack host	11	0·2	1·6 ,,
	Aug.	Died of starvation on tiny host	25	0·4	1·2 ,,

(3) *Habrocytus trypetae* (Fig. 10B)

The early stages of this chalcid parasite have been described elsewhere (Varley, 1937*a*). The eggs are laid in gall-cells containing larvae or puparia of the gall-fly, or in gall-cells already containing other parasites. When the host attacked is either a gall-fly pupa, or a larva of *Eurytoma curta* inside a puparium, some of the eggs may be laid outside the puparium,

and the parasite larvae die of starvation, being unable to penetrate the hard puparium.

Many eggs may be laid on a single host, but only one larva ever matures, because newly hatched larvae destroy any other eggs or larvae which they find. The degree of superparasitism is as great as, or greater than, would be expected if the egg distribution were random (Varley, 1941).

There may be two or three generations in the year. In 1935 adults emerged mainly in May, July and September. In the colder year 1936 they emerged in June and September.

these will have been included in the mortality of the gall-fly due to unknown causes.

Table 11 shows the numbers of *H. trypetae* found at different times of the year. The figures for the numbers of eggs laid per female have been calculated on the assumption that this parasite did not utilize alternative hosts outside the knapweed. The figures are quite consistent with this view, but, as *H. trypetae* has been recorded as a parasite of various species of insect,* the assumption requires justification.

In the region of the census the only gall-flies from other plants were a few *Urophora stylata* (Fab.) from

Table 11. *The effect of successive mortality factors on the numbers of the chalcid parasite* Habrocytus trypetae *found per sq.m. at Madingley*

			% killed	No. killed per sq.m.	No. alive per sq.m.
1935	Feb.	No. of larvae found	—	—	3·4 larvae
	May	Observed mortality	0	0	3·4 adults
	May	3·4 adults emerged per sq.m., 50% were females			
		Mean number of eggs laid: 20 per female	—	—	33 eggs
		Died due to superparasitism	64	21	12 larvae
		Failed to attack host	12·5	1·5	10·5 ,,
		Parasitized	21	2	—
		Died due to unknown causes		0·2	8·3 adults
	July	8·3 adults emerged per sq.m., 50% were females			
		Mean number of eggs laid: 0·24 per female	—	—	1 egg
		Died due to superparasitism	30	0·3	0·7 adults
	Sept.	0·7 adults emerged per sq.m., 50% were females			
		Mean number of eggs laid: 29 per female	—	—	10 eggs
		Died due to superparasitism	15	1·5	8·5 larvae
		Failed to attack host	23	2	6·5 ,,
		Destroyed by caterpillars	14	0·9	5·6 ,,
1936	Winter	Winter disappearance	61·5	3·4	2·2 ,,
		Destroyed by mice	64	1·4	0·8 adults
	June	0·8 adults emerged per sq.m., 50% were females			
		Mean number of eggs laid: 1·9 per female	—	—	0·76 eggs

After this the mean number did not rise above 1 in 10 sq.m., and further analysis is superfluous.

The newly emerged female is not sexually mature, and it first feeds on the host without laying eggs. It pushes the ovipositor down the neck of the flask-shaped gall until it stabs a host, which is then stung and paralysed. The female remains motionless for some time while a secretion hardens round the ovipositor to form a tube, from which the ovipositor is withdrawn. Through this tube the blood of the host exudes, and the parasite drinks it up. This method of feeding was first described by Lichtenstein (1921) for two other species of *Habrocytus*. It is also known from at least three other chalcid genera (*Eurytoma, Pteromalus* and *Spintherus*: see Clausen (1940) for references). Some of the hosts of *Habrocytus trypetae* in the knapweed were killed by this treatment. The flimsy broken feeding-tube is inconspicuous, and was probably overlooked in some cases; the spear thistle (*Cirsium vulgare* (Savi) Ten.), *Xyphosia miliaria* (Schr.) from the field thistle (*Cirsium arvense* (L.) Scop.), and *Icterica westermann* (Meig.) from the ragwort (*Senecio jacobaea* L.). In the knapweed the normal host was the gall-fly *Urophora jaceana*, while other occupants of the gall, such as *Eurytoma curta* were also attacked. However, *Habrocytus trypetae* was not found attacking the

* *Habrocytus trypetae* has been recorded as a parasite of the gall-flies *Terellia serratulae* (L.), *Urophora cardui* (L.), *Noëta pupillata* (Fall.) and from the moth *Sparganothis* (*Oenophthira*) *pilleriana* Schiff. and it has been reared from the flower-heads of species of the Composite genera *Centaurea, Carduus, Cirsium, Arctium* and *Hieracium*. The great difficulty in naming species of the genus *Habrocytus* perhaps makes some of the records doubtful.

non-gall-forming trypetids in the knapweed, such as *Chaetostomella cylindrica*, *Chaetorellia jaceae* and *Urophora quadrifasciata*. The first two of these species were indeed attacked by another quite distinct species of *Habrocytus*, *H. albipennis* (Walk.), and *Urophora quadrifasciata* was parasitized by another species to which Dr Ferrière was unable to give a name. This negative evidence is consistent with the assumption that this race of *Habrocytus trypetae* is restricted to hosts in the knapweed galls which remain in the standing flower-heads, and searches for its hosts neither in other parts of the knapweed, nor in other plants.

The census did not indicate whether the very small number of eggs laid in the knapweed in July 1935 was due to eggs being laid elsewhere. However, if females reared elsewhere had laid eggs in the 89 larvae attacked by *Habrocytus trypetae*, only 12, or 13·5%, were also parasitized by *Eurytoma curta*, whereas the percentage of gall-fly larvae containing *E. curta* was 45%. Both species were found together only one-third as frequently as would be expected if the *Habrocytus trypetae* females laid eggs on parasitized and healthy gall-fly larvae with equal readiness.

In May 1935, when there were only 23 hosts available per sq.m. in the standing flower-heads (Table 12), *H. trypetae* had a choice between larvae and pupae of both the gall-fly and *Eurytoma curta*. In this instance 82% of the gall-flies present, and 68% of the *E. curta* were attacked. The preference for the gall-fly is revealed by the difference in the percentages of survivors—18% of the gall-flies compared to 32% of the *E. curta*.

Table 12. *The effect of host density (expressed as the number of available hosts per sq.m.) on the host preference and the fecundity of* Habrocytus trypetae

When the number of hosts or the number of eggs laid is one per sq.m. or less the error in the estimates is likely to be large, and the figure must be taken as indicative only of the order of magnitude.

		Available hosts: Gall-fly larvae or pupae, *Urophora jaceana*		Available hosts: The chalcid, *Eurytoma curta*		Approximate no. of eggs laid per female of *Habrocytus trypetae*
		No. available per sq.m.	% attacked	No. available per sq.m.	% attacked	
1935	May	20	82	3·4	68	20
	July	0·1	—	0·1	—	0·24
	Sept.	64	12	48	1·4	29
1936	June	1	—	0·5	—	1·9

knapweed in September 1935 or September 1936 when hosts were abundantly available, the apparent oviposition rate of the few females known to have emerged from the knapweed might have been very large. Since it is quite reasonable to suppose that a single female *Habrocytus* could deposit 30 eggs in its lifetime, this provides no support for the idea that it attacks alternative hosts elsewhere.

Within the galls there are definite host preferences, and some of the data are given in Table 12. In September 1935 there were in each sq.m. 64 fully grown gall-fly larvae and 48 larvae of *Eurytoma curta* suitable for parasitization. Gall-fly larvae were preferred, and 12% of them were attacked, compared with only 1·4% of the *Eurytoma* larvae; which is a preference of nearly ten to one.

Unlike any other of the ectophagous parasites studied, *Habrocytus trypetae* even avoided laying eggs on gall-fly larvae which contained small larvae of *Eurytoma curta*. In August, 1935, eggs and larvae of *Habrocytus trypetae* were found on 89 gall-fly larvae in which the presence or absence of larvae of *Eurytoma curta* could be established. Of the

The number of eggs laid per female was very different in the different generations, and was clearly correlated with the changes in the density of available hosts (Table 12). The estimates are less accurate than those for the fecundity of the gall-fly, partly because of the smaller numbers involved, and also because in 1935 the three generations followed each other very quickly. The July and September generations so nearly overlapped that it was difficult in some cases to decide the generation to which empty egg-shells were to be counted. However, although the accuracy of the estimates is low, the changes observed are so large that they cannot be attributed entirely to errors in measurement.

In May and September 1935 the fecundity was estimated to be 20 and 29, when there were about 20 and 100 hosts available per sq.m. In July 1935 and June 1936, when the density of hosts was less than two per sq.m., the fecundity was less than 2 eggs per female. It is evident that the very low densities of available hosts greatly reduced the rate of increase of *Habrocytus trypetae*. This species, like *Eurytoma curta*, is therefore to be

regarded as a potential controlling factor of the population density of the gall-fly.

The action of *Habrocytus trypetae* upon the gall-fly is complicated by three facts. First, it accepts other hosts, such as the parasite *Eurytoma curta*, besides the gall-fly larvae. Secondly, it does not attack those hosts in fallen galls. Thirdly, the emergence of this species is not synchronized with the life history of the host. This last factor caused the virtual disappearance of *Habrocytus trypetae* from the census area during the period of observation. In 1935 the second generation of *H. trypetae* emerged very early, and was seeking hosts in July, when most gall-flies were in a stage unsuitable for parasitization —as adults, eggs, or very small larvae. The result was a reduction in the population density of *H. trypetae* from 8·3 adults per sq.m. in July to less than one adult per sq.m. in September of 1935. The following generation of this species was retarded in emergence until June by the cold spring of 1936, and only 0·8 adults emerged per sq.m. Almost all the hosts were then in the fallen galls and *H. trypetae* found so few to attack in the standing flower-heads that the number of parasites never exceeded one in 10 sq.m. during the rest of the summer of 1936. This catastrophic fall in the population density of this parasite was perhaps exceptional. In normal years *H. trypetae* probably emerges in May and August, and is able to find plenty of gall-fly larvae at a stage suitable for parasitization.

(4) *Torymus cyanimus* (Fig. 10C)

The larva of the chalcid *Torymus cyanimus* is an ectoparasite of the gall-fly larva. The early stages have been described elsewhere (Varley, 1937*a*). The eggs are usually laid in August, and though sometimes laid singly they are commonly laid upon the gall-fly larva in small groups (Varley, 1941). The first larva to hatch usually destroys the other eggs, but, although two larvae may feed upon the same host for a short time, only one larva comes to maturity. Development is rapid, and in 1935 some of the eggs laid in August gave rise to adults in September, while others passed the winter in the larval stage. The few small larvae found late in September may perhaps have been the progeny of these adults.

The emergence of adults from the hibernating larvae takes place in May of the following year. However, no fresh *Torymus* eggs or larvae were found on the available hosts in June or July, and no further fresh eggs or larvae of this species were seen until the next generation of gall-fly larvae became well grown in the following August. There are two possible explanations for this. First, *Torymus* may find some alternative host. The species has been recorded as a parasite of other gall-fly larvae, such as those of *Tephritis truncata* (Loew) and *Urophora cardui* (L.), but no other gall-flies were common in the area except *U. quadrifasciata*. Alternatively, the adult *Torymus* may wait from May until August, and then mature its eggs and attack the hosts. This has been shown by Flanders (1935) to happen with certain other chalcids, which wait for many months in the adult stage until hosts are available.

In the present work *Torymus cyanimus* has been found only in the knapweed gall-cells, and eggs were laid on healthy gall-fly larvae, and on larvae parasitized by *Eurytoma curta* quite indiscriminately. Occasionally eggs were also laid in or on puparia containing *E. curta* larvae.

The number of eggs, larvae and adults of *Torymus cyanimus* found in the census are shown in Table 13. Owing to the possibility of an alternation of hosts, the fecundity of this species has not been estimated. The mortality from superparasitism was very great in this species, and in addition a number of larvae failed in their attack on the host, which survived. The surviving hosts numbered sixteen in 1935 (six gall-fly larvae, nine larvae of *Eurytoma curta*, and one of *E. robusta*), and two gall-fly larvae and two larvae of *E. curta* in 1936.

(5) *Macroneura vesicularis* (Fig. 10E)

The life history and the larval stages of this common and polyphagous chalcid have been described by Morris (1938). The species was found only in the early summer in the old knapweed flower-heads, and the eggs were laid in the galls in May and June. The eggs were laid in small groups, and superparasitism was common (Varley, 1941), although only a single parasite could come to maturity on a single host. Superparasitism resulted in 63% mortality in 1935.

Each egg was found under a small silken pad. The larvae hatched and grew quickly, and became adults in July and August of the same year. These adults did not attack gall-fly larvae, but probably found alternative hosts in the knapweed stems, where larvae of the gall-wasp *Phanacis centaureae* were commonly parasitized by this species in the middle of the summer.

In May and June 1935 *Macroneura vesicularis* was fairly common in the census area. Eggs or larvae were found in 53 gall-cells, but in four other instances *M. vesicularis* was found to have attacked larvae or puparia of the small gall-fly *Urophora quadrifasciata*. In two other instances the host was a puparium of the related gall-fly *Chaetorellia jaceae*. The cells formed by the knapweed gall-fly were apparently its chief habitat in the knapweed at this season.

In seven of the 53 cases the gall-fly larva was the host, and in six of these the attack was

successful. But only one out of another seven attacks on gall-fly puparia was successful. In one case this species competed unsuccessfully with *Torymus cyanimus* for the same gall-fly larva, and in 38 cases it competed with *Habrocytus trypetae* for the same gall-fly larva or pupa. *Macroneura* was the victor in ten of these cases, and *Habrocytus* in 22 cases, but in three of the latter the *Habrocytus* larva was subsequently destroyed by *Tetrastichus* sp. B, and in six cases both species were unsuccessful and failed to mature. Thus only 17 of the 53 attacks on hosts in the gall was a pupa of the moth *Metzneria metzneriella*, whose larva had fed in the gall.

(6) *Tetrastichus* sp. B (Fig. 10D)

Specimens of this unnamed species have been deposited in the British Museum Collections.

Tetrastichus sp. B has at least two generations in the year, and the main emergences seem to take place in June and August. The adults which emerge in June attack the hosts in the old-standing flower-heads of the knapweed, and various species are parasitized. The larvae are gregarious endoparasites,

Table 13. *The effect of successive mortality factors on the numbers of the chalcid parasite* Torymus cyanimus *found per sq.m. at Madingley*

			% killed	No. killed per sq.m.	No. alive per sq.m.
1934	Sept.	Eggs laid per sq.m.	—	—	9 eggs
		Died due to superparasitism	62	5·6	3·4 larvae
		Failed to attack host	15	0·5	2·9 ,,
		Destroyed by caterpillars	3	0·1	2·8 ,,
1935	Winter	Winter disappearance not estimated	—	?	2·8 larvae
	April	Pupae or adults died	10	0·3	2·5 adults
	May	2·5 adults emerged per sq.m.			
	Aug.	Eggs laid per sq.m.	—	—	7·7 eggs
		Died due to superparasitism	43	3·3	4·4 larvae
		Failed to attack host	11	0·5	3·9 ,,
	Sept.	Died due to unknown causes	6·5	0·25	3·65 ,,
		0·8 adults emerged per sq.m.	—	—	2·85 ,,
1936	Winter	Winter disappearance	61·5	1·75	1·10 ,,
		Destroyed by mice	64	0·7	0·4 pupae
	May	0·4 adults emerged per sq.m.			
	Aug.	Eggs laid per sq.m.	—	—	5·6 eggs
		Died due to superparasitism	65	3·65	1·95 larvae
		Failed to attack host	10	0·2	1·75 ,,
	Sept.	Died due to unknown causes	11	0·15	—
		Killed by *Habrocytus trypetae*		0·05	1·55 larvae

were successful, and the mortality was 68%. The relative time of attack seems to be the chief factor determining which of the competing parasites will be successful, and in general the last parasite to attack was the victor. In some cases larvae of *Macroneura* were found feeding on fifth instar larvae of *Habrocytus trypetae*, and one was found feeding on a *Habrocytus* adult which had only recently emerged from its pupal skin, and was still in the gall-cell. *Habrocytus* was never found feeding on a larva of *Macroneura*.

In the summer of 1936 only seven gall-cells were found containing *Macroneura*. Of the seven hosts two were larvae and three were puparia of the gall-fly, and one was a puparium containing *Eurytoma curta*, which survived the attack. The seventh host and any number between three and twenty may feed in the same host. The adults emerging in August usually attack gall-fly larvae in the fresh galls, and their progeny hibernate as larvae in the dry skin of the host.

In February 1935 22 hosts were found attacked by this parasite; 19 hosts were gall-fly larvae, two were *Eurytoma curta*, and in one instance the larva of the ichneumon fly, *Ephialtes buolianae*, was the host. These parasites became adult in June, and of 14 hosts found attacked by them in the standing flower-heads six were gall-fly larvae, and eight were larvae or pupae of the chalcid *Habrocytus trypetae*. In the next generation of flower-heads eight gall-fly larvae, four *Eurytoma curta*, one *E. robusta* and one *Habrocytus trypetae*

were found attacked by October. Few or no further instances of attack by this species were found until October 1936, when three gall-fly larvae were found attacked. Perhaps the fall in numbers of this species was due to lack of available hosts, as was the similar fall in *Habrocytus trypetae*, but the parasite was not common enough for much information to be available on this point.

Two other tetrastichine chalcids, *Aprostocetus daira* Walk. and *Tetrastichus brevicornis*,* were found as occasional parasites of the gall-fly larvae. The larvae of *Aprostocetus daira* were more commonly found as gregarious endoparasites of the related gall-fly *Chaetorellia jaceae*, but its larvae were not distinguishable from those of *Tetrastichus* B. *T. brevicornis* larvae were recognizable because they were not found in the skin of the dead host. They were probably ectophagous.

(*e*) *Mortality due to caterpillars*

The caterpillars of three species of moths, *Eucosma hohenwartiana*, *Metzneria metzneriella* and *Euxanthis straminea* (Fig. 11), live in the knapweed flower-heads, and if they encounter a gall in the flower-head they almost invariably enter it. They feed on the succulent gall tissue, tunnel from one cell to another, and destroy the contents. Gall-fly larvae were occasionally found soon after they had been killed in this way, and the wounds made by the caterpillars were clearly seen. When a caterpillar has finished feeding on a gall-cell, it is left empty save for a mass of dry faecal matter.

In 1935 three-fifths of the destruction of the galls by caterpillars was due to *Eucosma hohenwartiana*, and the remainder to *Metzneria metzneriella*. In 1936 *Eucosma* was responsible for three-quarters of the caterpillar damage. *Euxanthis straminea* was very rare in the census area; a few galls were found which had been damaged by it in the summer of 1934, but none was found either in 1935 or 1936, although the species was fairly common near by.

(1) *Eucosma hohenwartiana* (Fig. 11 A)

The moths are on the wing in the last half of July. In daytime they rest on the flower-heads and leaves of the knapweed, and the eggs are laid on the bracts of the flower-heads. The young caterpillars enter the flower-heads and feed on the contents, which they web together with silk in a characteristic way. If a caterpillar meets a gall, it enters and feeds largely on the gall tissues, and kills any gall-fly larvae it encounters in the cells. When fully fed in September the caterpillar leaves the flower-head and pupates in the soil, from which it emerges as a moth in the following July.

Apparently the caterpillar completes its growth in a single flower-head, and does not move into a second. Occasionally two caterpillars were found in the same flower-head.

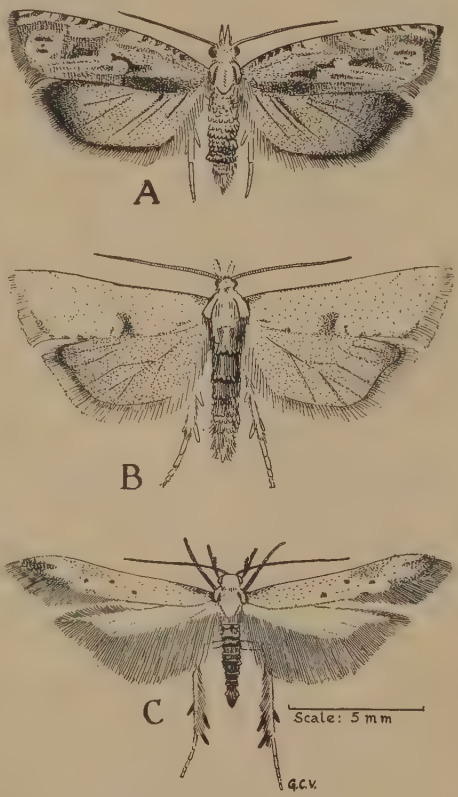

Fig. 11. Moths from knapweed flower-heads.

A. *Eucosma hohenwartiana*: forewings pale greyish brown, with darker markings; hindwings greyish brown.

B. *Euxanthis straminea*: forewings yellowish buff, with brown central shading; hindwings pale grey.

C. *Metzneria metzneriella*: forewings russet brown with grey-brown markings; hindwings pale grey.

The percentage of flower-heads attacked by *Eucosma* caterpillars was 17·5 % in 1935, and 23·5 % in 1936, and these were approximately the proportions of galls affected by them, indicating that the caterpillars and the galls were distributed independently. In the galls attacked by *Eucosma* 45 % of the gall-cells were destroyed.

* *Tetrastichus brevicornis* appears to be new to the British list.

Very few *Eucosma* caterpillars were found dead in the flower-heads. In October 1935 three dead caterpillars were found in 251 flower-heads which had contained this species, and in August and September 1936 six dead caterpillars were found in 657 such flower-heads.

Some of the caterpillars were parasitized by ichneumonoid larvae. One was found attacked by the ectophagous pimpline *Ephialtes buolianae* Hartig. All the live caterpillars found in 1936 were dissected and examined for internal parasites. Of 243 examined 28 contained first instar larvae of ichneumonoids. There were 18 *Glypta* larvae (*Glypta longicauda* Hartig and *G. vulnerator* Gr. were both found as adults seeking hosts in knapweed flower-heads). Two of the *Glypta* larvae were dead, one of them being in the same caterpillar as a live *Glypta* larva.

One of the 28 *Eucosma* caterpillars contained the first instar larva of *Omorga ensator* (Gr.), and five had larvae of *Macrocentrus nidulator* Nees. Three contained unknown larvae of two different species. In other localities *Eucosma* caterpillars were attacked by various ectophagous ichneumonoid larvae, such as *Ephialtes brevicornis* (Gr.), and *Microbracon marshalli* Szepl., but none of these was found in the census, although they were quite common about a quarter of a mile away.

(2) *Metzneria metzneriella* (Fig. 11 C)

The moths are to be seen in the daytime on the leaves and flower-heads of the knapweed in July, and the eggs are laid on the bracts. The caterpillars feed on the young florets, and may also tunnel a few millimetres down into the stem. They become fully fed in September and October, and make a silken gallery or cocoon in which they pass the winter inside the flower-head, where they eventually pupate in the following May.

Metzneria caterpillars were found in 5·8% of the fresh flower-heads in October 1935, and in 3·8% in 1936. These percentages are also approximately the percentage of galls attacked. If a *Metzneria* caterpillar is in a galled flower-head, it almost invariably takes up residence in the gall, and eventually makes its cocoon there. In these flower-heads attacked by *Metzneria* about 80% of the gall-cells were destroyed, compared with 45% for *Eucosma*.

The mortality of the *Metzneria* caterpillars was quite small in the flower-heads up till October. Only three dead caterpillars were found out of a total of 83 in 10 sq.m. in October 1935. In the summer of 1936 this same generation of flower-heads was examined, and the number of *Metzneria* caterpillars found had dropped from 8·3 to 1·5 per sq.m., due to winter disappearance and mice. Out of a total of 54 old flower-heads found in the summer of 1935 which contained cocoons of *Metzneria*, two contained live caterpillars, eleven contained live pupae, and the moths had emerged from nine. Of the 59% mortality, 23 individuals had disappeared due to unknown causes, seven were parasitized by the braconid *Neochelonella sulcata*, and one pupa had been killed by the chalcid *Macroneura vesicularis*.

The mortality was more carefully studied in the next year, late in the summer of 1936, when all the caterpillars found were examined for internal ichneumonoid parasites. Three dead caterpillars were found, and dissection of 107 caterpillars found alive revealed 17 first instar larvae of *Neochelonella sulcata*, two of *Macrocentrus nidulator*, and one of *Omorga ensator*, making a total of 23, or 21% parasitized caterpillars. Elsewhere this species was parasitized by the *Microbracon* and *Ephialtes* species which also attacked *Eucosma*.

(3) *Euxanthis straminea* (Fig. 11 B)

This double-brooded species passes the winter as a caterpillar in the shoots of knapweed. In June and July caterpillars of the second generation enter the small flower-heads, always leaving a hole in the stem just beneath the bracts.

The species was present in less than 1% of the flower-heads in 1935 and 1936, and no galls were destroyed in this period. However, a small number was damaged by them in the summer of 1934.

PART 4

DISCUSSION AND CONCLUSIONS

This study of the community in the black knapweed flower-heads has shown the numerical effect of the various biotic and climatic factors on the population density of the knapweed gall-fly over a period of 2 years. By the analysis of this tangled skein of relationships we wish to find an answer to the question asked in the introduction: What factors control the population density of the knapweed gall-fly in nature, and how do they operate?

It has already been pointed out that controlling factors must be density dependent. They are the factors responsible for maintaining a balance in the population density, by acting more severely when the population density is high, and less severely when the population density is below the average. However, some confusion has arisen in the literature since the word 'control' has been given different meanings by different workers. By 'control' many economic entomologists mean the maintenance of the population density of a pest below a level at which it does economic damage. Some now use it simply as a synonym for destruction.

Bodenheimer (1938, p. 105), in a discussion of the relative values of climatic and biotic factors in the control of animal populations, claims that 'all factors are of destructive value in direct proportion to the percentage per stage destroyed by each'. On this view it is sufficient in the case of the knapweed gall-fly to examine Table 8, in which the destructive value of the various factors can be seen at a glance. The most important are: destruction by mice and winter disappearance, which in the winter of 1935–6 destroyed 64% and 61·5% of the gall-fly larvae respectively; *Habrocytus trypetae*, which destroyed nearly 60% of the gall-fly larvae and pupae in May and June of 1935; flooding, which caused 44% destruction in July 1936; and *Eurytoma curta*, which parasitized 45·5 of the young larvae in July 1935.

Had any of these destructive factors not operated, the population density of gall-flies emerging from that generation of larvae or pupae would indeed have been proportionately greater. But Bodenheimer's claim applies only to the immediate effect in one generation. It is not necessarily true that the best method of reducing the average population density of the knapweed gall-fly over a number of years would be the artificial intensification of any one of these factors. Volterra's third law, the law of disturbance of the averages, states that if a predator and prey are in equilibrium, the equilibrium population density of the prey will be *increased* if equal proportions of the predator and its prey are killed in each generation.

Before it can be decided whether the intensification of a factor which causes the destruction of a pest will tend either to reduce or to increase the mean population density of the pest, further facts are needed. If in addition to destroying the pest, it destroys any parasitic species which may act as a controlling factor, then its long-term effect may be as Volterra predicts for predator and prey. For the special case of insects which have discrete generations, the interaction between one factor and another can conveniently be investigated by means of Nicholson & Bailey's theory of balance of animal populations, once the necessary fundamental information about the factors is available from suitable census data.

The first step in the analysis is to find which of the potential controlling factors is in fact operating. The three factors which appear to have the right properties are the density-dependent early larval mortality, and the two common chalcid parasites, *Eurytoma curta* and *Habrocytus trypetae*, which act as delayed density-dependent factors.

The early larval mortality was due partly to competition between the larvae in the same flower-head before the formation of the gall. Evidence has already been presented which shows at least for 1935 that the mortality was rather higher in those flower-heads containing many larvae than in those containing only one or two. Thus the early larval mortality is density dependent, and overcrowding at this stage is potentially able to limit the population density. However, the degree of competition within a single flower-head is not simply proportional to the population density, but will rise only when more than one egg batch is commonly laid in the same flower-head. Although the percentage of flower-heads galled was 44% in 1935 and only 8% in 1936, the mean number of eggs found in flower-heads was 3·02 in 1935 and 3·04 in 1936. Hence the degree of competition was the same in the 2 years.

The population density of the gall-fly would begin to increase the larval competition within the flower-heads only when the percentage of flower-heads attacked rose to well over 50%. But in none of the many localities where preliminary census work was undertaken was this figure reached. Clearly some other factors prevent the population density rising to such a level that competition between larvae is effective as a controlling factor.

Had this crowding factor alone been responsible for the limitation of the population density, almost 100% of the flower-heads might have been galled. In the census as many as ten gall-cells were found in a single flower-head, and sixteen were once found under insectary conditions. Taking a fairly conservative figure of 150 flower-heads per sq.m. in the census area, population densities as high as 2400 larvae per sq.m. would be possible, which is sixteen times greater than the highest larval population density found in the field, and 350 times greater than the largest adult population.

The two potential controlling factors remaining are the delayed density-dependent factors *Eurytoma curta* and *Habrocytus trypetae*. Their fecundity has been shown to be greatly influenced by changes in the population density of gall-fly larvae, which acts upon them as a density-dependent factor. The estimated number of eggs laid per female *Eurytoma curta* fell from 63 in 1935 to 8·4 in 1936 in response to a cold summer and a three-fold fall in the larval population of gall-flies. This is the kind of change expected on the theory of Nicholson and Bailey, but it is possible to go further and examine the agreement between some of the fundamental assumptions of the theory and the field data.

Nicholson and Bailey assume that parasites search for their hosts at random. Various meanings have been attached to the term 'random', and an attempt to clarify this has been made by Varley (1941), where it is shown that parasites which seek their hosts by random movements may produce a distribution of progeny amongst the available hosts which is non-random in space. The data from 20 sq.m. examined

in the summer of 1935 show a significant correlation between the percentage of parasitism by *E. curta* and the fraction of flower-heads containing galls. However, this spatial discrepancy was of a kind which did not greatly affect the numerical result of parasitism. For common parasites in a limited area such as the census area it is concluded that search is random to a first approximation.

The idea of random search has been attacked by Thompson (1939) whose main argument seems to be based on a misunderstanding of Nicholson's use of the term 'random'. Thompson argues that search cannot be random since parasites tend to select definite host species for attack. But by random search Nicholson & Bailey meant a search for the particular host species. Their mathematical formulation requires simply that the rate of discovering new hosts at any instant should be proportional to the product of the population densities of the searching parasites and the undiscovered hosts.

The second basic assumption of Nicholson & Bailey's theory is that parasites in their random search for hosts search an area, termed the *area of discovery*, the average size of which is constant and independent of the population densities of hosts and parasites. In this area all the hosts are supposed to be found and parasitized. The area of discovery of *E. curta* can be estimated for two generations by substitution of values in the formula given by Nicholson & Bailey (1935, p. 555), which can be written:

$$a=\frac{2\cdot3}{p}\log\frac{u_1}{u}, \qquad (1)$$

where a is the area of discovery, p the population density of adult parasites, and u_1 and u the population density of host larvae before and after parasitization, so that u/u_1 is the fraction of hosts which escapes parasitization.

In 1935 the population density of *E. curta* was estimated to be $p=2\cdot0$ adults per sq.m., and 45·5 % of the gall-fly larvae were parasitized, leaving the fraction of survivors $u/u_1=0\cdot545$. In 1936 the figures were $p=1\cdot66$ adults per sq.m., and the fraction of hosts escaping parasitism was 0·73. Substituting these values in the equation the area of discovery of *E. curta* works out at 0·31 sq.m. in 1935 and 0·19 sq.m. in 1936. Possibly the much colder July in 1936 may have been responsible for a reduction in the area of discovery, but the difference between these estimates is not significant. Clearly the area of discovery of *E. curta* is much less affected by the changes in host density than is its fecundity, in which there was a significant seven-fold change. The average value for the area of discovery will be taken to be 0·25 sq.m. As half the adults of *E. curta* are males the area of discovery of a female must be 0·5 sq.m., so that a female must be able to parasitize a number of hosts equal to that in about 100 flower-heads. This does not seem an unreasonable figure for the whole life of a female parasite.

Estimates of the area of discovery of *Habrocytus trypetae* can be made for the generations emerging in May and September 1935. Insufficient data were available at other times. In May 1935 the number of adults which emerged per sq.m. was 3·4 and eggs were laid on 80 % of the available hosts, leaving 0·2 as the fraction of hosts surviving. From equation (1) the area of discovery works out at 0·47 sq.m. At this time the number of flower-heads still available on the standing stems was 120 per sq.m., of which 18 were galled. As the proportion of females was 0·5, the area of discovery of *H. trypetae* females is equivalent to 113 old flower-heads.

In September 1935 a less accurate estimate is possible. The number of adult *H. trypetae* was estimated to be 0·7 per sq.m., and they attacked 12 % of the available hosts, leaving a fraction of 0·88 survivors. The area of discovery works out at 0·18 sq.m. The mean number of flower-heads in the ten samples on which these figures are based was 190 per sq.m., so the area of discovery can be expressed as 80 fresh flower-heads per female. These estimates of the area of discovery, when expressed in terms of flower-heads; are not significantly different. In September all the flower-heads contained a number of fruits, and a mass of paraphyses between them, often surmounted by the dead florets. In May the remaining flower-heads were dry and dead; many were indeed dry circlets of bracts only, from which the contents had fallen to the ground. Hence it might be expected that the time taken to search flower-heads in May would be less than the time required in September, making the area of discovery a smaller number of flower-heads in September than in May.

It cannot be claimed that these data demonstrate the accuracy of the assumptions made by Nicholson & Bailey. The assumptions made in the mathematical theories which are used in biology are made rather for their mathematical simplicity than because they are believed to be exact. Indeed, it is inconceivable that the area of discovery of a parasite remains absolutely constant over a very wide range of host and parasite population densities. At high host densities the parasite will be limited by egg supply. However, over the narrow range of host and parasite densities observed in the census area, the data for both species are in broad agreement with the assumptions of Nicholson & Bailey. They do not agree nearly so well with the idea that the fecundity of a parasite is constant, which is fundamental to the only other mathematical theory which can readily be applied to the interaction between such parasites and hosts with synchronized generations (Thomp-

son, 1924, etc.). Thompson's theory applies only when host density is so high that the parasite's rate of increase is limited by egg supply. The parasite is then not density dependent.

With caution, therefore, Nicholson & Bailey's theory may be used to study the interactions between the different factors causing mortality.

To attempt to predict over many generations the course of interaction between the various species affecting the gall-flies would be useless, owing to the unpredictable effects of weather and other factors. Furthermore, any errors in the calculation would be cumulative. However, the theory of Nicholson & Bailey can be used more simply. It is possible to calculate the population density of parasite and host, assuming them to be in the steady state. This involves making a prediction only one generation ahead, so that the effect of any errors is minimized.

The steady state is the condition in which the host and its parasite are in exact equilibrium. The host density is such that the parasite can only just maintain its numbers from generation to generation, and the parasite's density is such that it is just sufficient to kill off the surplus host progeny. The actual population density would be expected to oscillate about this value calculated for the steady state, and the mean population density over a number of generations would be expected to be close to this value.

The following section of this paper is admittedly speculative, but even if the conclusions reached have little quantitative accuracy and indicate trends only, they are still of considerable interest.

Using the data supplied by the census, it is possible to calculate the steady state which *Eurytoma curta* could maintain if it were the only mortality factor operating on the gall-fly larvae after gall-formation. The only attribute of *E. curta* for which a value is required is the area of discovery, which has an average value of 0·25 sq.m. A value is also required for the natural rate of increase of the gall-fly, which can be found at once from Table 8. In 1935 the number of gall-flies which emerged per sq.m. was 6·9, and they produced 147·6 suitable hosts per sq.m., which is a 21-fold increase. In 1936 two gall-flies produced 28 suitable hosts per sq.m., giving a rate of increase of 14. This change may well have been caused by weather differences. The natural rate of increase will therefore be given a mean value of 18. In the steady state this 18-fold increase must be balanced by a mortality of $17/18 = 94{\cdot}5\,\%$ in each generation. The population density p of adult *E. curta* needed to discover 94·5 % of the gall-fly larvae can be found from equation (1), since the term (u_1/u), the ratio of the population densities of host larvae before and after parasitization, must be equal to the natural rate of increase (F), which equals 18. Hence we can write

$$p = \frac{2{\cdot}3}{a} \log F. \qquad (2)$$

Substituting values for a and F we find the steady density of adult *E. curta* to be 11·5 per sq.m. All the gall-fly larvae which are parasitized are supposed to give rise to adults of *E. curta*, hence $p = h(F-1)$. Substituting this in (2) we find the steady density of adult gall-flies to be

$$h = \frac{2{\cdot}3 \log F}{a(F-1)}. \qquad (3)$$

Substituting values for F and a the steady density of the host works out at 0·68 gall-flies per sq.m.

This calculated estimate of the steady density of gall-flies is far below the values of the population found in the census in the 2 years, which were 6·9 gall-flies per sq.m. in 1935 and 2·0 per sq.m. in 1936. At the same time the steady density calculated for *E. curta* was 11·5 adults per sq.m. compared with 2·0 and 1·66 adults per sq.m. in the census. In the census, however, *E. curta* caused only 45·5 % mortality of the gall-fly larvae in 1935, and 27 % in 1936, whereas in these calculations it has been assumed that *E. curta* was responsible for 94·5 % mortality. It remains to be seen what effect the other mortality factors might have on the steady state.

The mortality factors can be considered under three headings: (1) non-parasitic factors acting specifically on the gall-fly; (2) specific parasites acting only on the gall-fly; (3) non-specific factors, acting both on the gall-fly and on its parasites.

(1) The specific non-parasitic factors either alter the fecundity of the adult gall-flies, or cause mortality at some stage in the life history. The factors affecting the fecundity are: (*a*) the weather during the oviposition period; (*b*) the amount of food available to the adult gall-flies; (*c*) the population density of gall-flies.

In 1936 the population density of the gall-flies was so low that interspecific mating was common during part of the breeding season, and about 8 % of the egg batches were infertile. Population density acted here as a density-dependent factor of a negative type, since its destructive effect was inversely proportional to the population density. However, the total effect was not large at the population densities observed. This factor must in fact always operate at the beginning and end of the breeding season.

Changes in weather and food supply must cause the fecundity to vary from year to year in an irregular manner. This will prevent the population density from reaching a steady value, even if it had a tendency to do so.

The mortality factors which come into this category are the egg mortality, the early larval

mortality, and any mortality due to functional disease which has been included in 'unknown causes'. These factors together produced a total of 30% mortality in the summer of 1935, and 40% in 1936. They have been allowed for in the estimation of the natural rate of increase of the gall-fly.

(2) The only specific parasite of the gall-fly is *E. curta*, whose effect is already under discussion.

(3) Chief amongst the non-specific mortality factors which act indiscriminately on the gall-fly and its parasites are mice, winter disappearance, and caterpillars. The effects of these factors were identical so far as could be determined both on the gall-fly and on *E. curta*. None of these factors can be regarded as density dependent, since neither mice nor caterpillars rely on the contents of the gall for their main food.

Another non-specific factor is summer flooding, which Table 8 shows to have destroyed 44% of the gall-fly pupae, while Table 9 gives the destruction of *E. curta* as 53%. The difference here may perhaps be due to physiological differences between the species, but it is too small to be statistically significant. This factor operated only in the summer of 1936.

The non-specific chalcid parasites *E. robusta* and *Torymus cyanimus* attacked the gall-fly larvae in August when some of them contained small larvae of *Eurytoma curta*. Such parasitized gall-fly larvae were attacked just as readily as healthy ones. The chalcids *Macroneura vesicularis* and *Tetrastichus* sp. B parasitized both *Eurytoma curta* and the gall-fly indiscriminately. Both had at least two generations in the year, but their effect was greatest in the early summer, when they attacked the contents of the old galls on the standing stems. *Habrocytus trypetae* shows preference for the larvae and pupae of the gall-fly, and so cannot be regarded as non-specific. It will be given separate consideration.

Probably all the non-specific parasites are capable of acting as delayed density dependent factors; but they were not sufficiently common in the census area to destroy a high percentage of the gall-flies. Although there was no evidence that either *Eurytoma curta* or *Tetrastichus* spp. used hosts outside the knapweed, *Macroneura* and possibly *Torymus cyanimus* had alternative hosts elsewhere, and so were not entirely dependent on the gall-fly population. In the light of these facts, none of the latter parasites is considered to be acting as effective controlling agents in the census area. In so far as they destroy *Eurytoma curta* and the gall-fly in proportion to the relative numbers present, their effect will be the same as that of the other non-specific mortality factors. The percentages of mortality caused by all the non-specific factors, whether parasitic or otherwise, can therefore be summed together.

The total effect of the non-specific factors can be obtained from Tables 8 and 9. In the 1934–5 generation the non-specific mortality (marked with an asterisk) amounted to $5/35 = 27{\cdot}4\%$ before the winter, followed by 18·5% killed by mice, and $0{\cdot}5/17{\cdot}4 = 3\%$ killed by parasites. These together amount to 43%. The true figure would be higher, if the winter disappearance had been estimated. If the partly specific mortality due to *Habrocytus trypetae* is included, it brings the total non-specific mortality to 76·4%.

In the 1935–6 generation Table 8 shows that $28/79{\cdot}6 = 35{\cdot}2\%$ of the gall-fly larvae were killed by non-specific factors in August and September. Winter disappearance removed 61·5%, mice destroyed 64%, birds, *Macroneura* and *Tetrastichus* together killed $0{\cdot}9/5{\cdot}2 = 17\%$, and the summer floods a further 44%, which together give a total mortality of 95·8% for the non-specific factors. The figure works out at 96% for the mortality of *Eurytoma curta* by the same factors in Table 9.

In the 1936–7 generation 34% non-specific mortality had occurred by September.

The available data do not allow us to assign an average value for the non-specific mortality. It is produced by a series of diverse factors, each of which varies in severity from year to year. But, except for that part caused by parasites, there is no reason to suppose that the variations in severity will be influenced by the population density of either the gall-fly or *E. curta*. It will be instructive to find the effects different average values of non-specific mortality might have on the balance between the gall-fly and *E. curta*.

In the steady state the gall-fly must have a mortality of 94·5% to balance the 18-fold natural rate of increase. If after the attack by *E. curta* non-specific mortality factors destroy a fixed percentage of gall-fly larvae so that a fraction x survive, then *E. curta* will need to destroy only $(1 - 1/18x)$ of the gall-fly larvae instead of 17/18. The successive changes in the population densities of gall-flies and of *E. curta* during one generation can be represented diagrammatically as follows:

	Adults	Larvae (u_1)	Surviving larvae (u)	Adults
Successive gall-fly densities	h	$\longrightarrow hF$	$\longrightarrow D \rightarrow Dx$	$\longrightarrow Dx = h$
		$\downarrow$		
Successive *E. curta* densities	p	$\longrightarrow hF - D$	$\longrightarrow (hF - D)\,x$	$\longrightarrow (hF - D)\,x = p$

If the steady density of adult gall-flies is h per sq.m., hF larvae will be found, F being the natural rate of increase, 18. These larvae are attacked by *E. curta*. Assuming that the number remaining unparasitized is D, then $hF-D$ must be parasitized, and contain larvae of *E. curta*. The fraction x of these survive in each case and emerge as adults. In the steady state the number of adults in successive generations is the same, so we can write

$$h=Dx, \quad (4)$$

$$p=(hF-D)\,x. \quad (5)$$

from which the values for the population densities can be obtained by putting in values for a, F and x.

Similarly, the steady densities of the gall-fly and its parasite *E. curta* can be calculated for other conditions in which different types of mortality operate. Various conditions are compared in Table 14 with the values of the steady density calculated for different percentages of non-specific mortality. Table 14A shows the steady state which *E. curta* could maintain alone. Mortality acting only on the gall-fly (B and C) increases slightly the steady

Table 14. *The theoretical effect of different types of mortality factors on the balance between the gall-fly* Urophora jaceana *and its chalcid parasite* Eurytoma curta

The natural rate of increase of the gall-fly is taken as 18, and the area of discovery of *Eurytoma curta* 0·25 sq.m.

	Steady density of the gall-fly		Steady density of adult *Eurytoma curta*	Percentage of gall-fly larvae parasitized
	Adults per sq.m.	Available larvae		
A. *Eurytoma curta* acting alone	0·68	12·2	11·5	94·5
Mortality acting only on the gall-flies:				
B. Before *Eurytoma* attacks				
(1) 50% mortality	1·1	10	8·8	89
(2) 90% mortality	2·9	5·3	2·4	45
(3) 92% mortality	3·3	4·8	1·5	31
C. After *Eurytoma* attacks				
(1) 50% mortality	0·55	10	8·8	89
(2) 90% mortality	0·29	5·3	2·4	45
(3) 92% mortality	0·26	4·8	1·5	31
D. Mortality acting only on *Eurytoma*:				
(1) 50% mortality	1·35	24·4	11·5	94·5
(2) 90% mortality	6·8	122	11·5	94·5
(3) 92% mortality	8·5	153	11·5	94·5
E. Non-specific mortality acting on gall-flies and *Eurytoma* after its attack:				
(1) 50% mortality	1·1	20	8·8	89
(2) 90% mortality	2·9	53	2·4	45
(3) 92% mortality	3·3	60	1·5	31
(4) Over 94·5% mortality	0	0	0	—
F. Census data for comparison:				
1935	6·9	147	1·9	42
1936	2	28	1·5	27

The change in the population density of the gall-fly from hF to D per sq.m. is due to parasitism by *E. curta*. Substituting for u_1/u in equation (1) we can write

$$p=\frac{2\cdot3}{a}\log\frac{hF}{D}. \quad (6)$$

The unknown D can be eliminated from equations (5) and (6) by substituting $D=h/x$ from (4). Hence we have two equations

$$p=\frac{2\cdot3}{a}\log Fx, \quad (7)$$

$$h=\frac{p}{Fx-1}, \quad (8)$$

densities of available gall-fly larvae, but decreases the steady density of *E. curta*. The result (B) is in accordance with conclusion 7 of Nicholson (1933, p. 150). Mortality acting only on *E. curta* leaves its steady density unchanged, but greatly increases that of the gall-fly (D). Compare Nicholson's conclusion 5.

The most important conclusion is that increasing percentages of non-specific mortality (E) acting equally on both species, *increase* the steady population density of gall-flies, and decrease the steady population density of *E. curta*. This is in accordance with Volterra's law of disturbance of the averages.

A comparison between the calculated values and the census data (F) shows a striking agreement. With a non-specific mortality of 92% the calculated steady density of gall-flies is 3·3, compared with 6·9 and 2·0 in 1935 and 1936. The number of available larvae per sq.m. is 60, compared with 147 and 28 in the census. The population density of *E. curta* is 1·5 per sq.m., compared with 2·0 and 1·66, and the percentage of parasitism by *E. curta* is 31% compared with 45 and 27% in the 2 years. Thus with 92% non-specific mortality acting with *E. curta* all the calculated figures are between the census figures for the 2 years. In none of the other conditions considered in A–D of Table 14 is this so.

This correspondence between the calculated steady densities and the census data has been achieved by giving the non-specific mortality a fixed value of 92%. Doubtless the mean figure for this mortality must be less than 96%, which was the estimate for 1935–6, since with an 18-fold natural rate of increase this would eventually cause extinction of both gall-fly and its parasites. Possibly the absence of the gall-fly from some localities may be due to high values of non-specific mortality.

The effects of the remainder of the observed mortality must now be considered. Table 8 shows that after gall-formation the factors killing gall-fly larvae which remain are *Habrocytus trypetae*, the predaceous gall-midge *Lestodiplosis miki*, and unknown causes. Their percentage values are small compared with the total non-specific mortality.

Unknown causes resulted in 5% empty gall-cells in 1934, 2% in 1935 and 4·3% in 1936. This factor would have a very small effect of the kind shown in Table 14B—increasing slightly the steady density of the gall-flies, and decreasing those of the larvae and of *Eurytoma curta*.

After the winter of 1936 unknown causes destroyed 26% of the gall-fly larvae. Although this same factor did not operate on *E. curta*, Table 9 shows that at this time 33% of the *Eurytoma* were recorded as 'missing'. If two separate factors destroy the same percentage of host and parasite, the effect on the balance is the same as if a single non-specific factor had been responsible for the destruction of both species. This mortality can therefore be added to the non-specific mortality, and would increase its effect.

Habrocytus trypetae has been shown to be potentially a controlling agent, but in the census area its influence was too small to be effective. During the course of the census the numbers of this species fell catastrophically, owing to its lack of synchronization with the period of host availability, and its failure to attack these hosts in the fallen galls. There is no need to publish detailed results of the calculations which have been made for the action of this species on the gall-fly. A series of formulae similar to those used for *Eurytoma curta* can easily be derived to fit the life history of *Habrocytus trypetae* and the changes in host availability. It is enough here to state the general conclusions reached, which are:

(1) If *H. trypetae* alone acts on the gall-fly, and all the gall-fly larvae remain available for parasitization, the calculated steady density of the gall-flies is independent of the number of generations of *H. trypetae* per year. Since some gall-fly larvae are not in fact available in early summer, the emergence of *H. trypetae* at this time reduces its efficiency as a controlling agent. Thus, according to this application of Nicholson & Bailey's theory, a parasite with two or more generations to every one of the host cannot be more efficient than another species with the same area of discovery which has one generation synchronized with the period of maximum host availability. If the parasite with many generations commonly emerges at times when a proportion of the hosts are not suitable for parasitization, then, though it may be able to increase more rapidly in a high host population, it may be very inefficient as a controlling agent.

(2) The critical factors for the success of *H. trypetae* in the field are the proportion of the hosts available, and the proportion of the non-available hosts which survive.

(3) If *H. trypetae* and *Eurytoma curta* both attack the gall-flies, the result of the competition between them depends on the host selection of *Habrocytus trypetae*. The areas of discovery of the two species are about equal. Hence if *H. trypetae* attacked only gall-fly larvae as hosts, it would in time be completely displaced by *Eurytoma curta*. On the other hand, if *Habrocytus trypetae* attacked *Eurytoma curta* and the gall-fly with equal readiness, it would itself displace that species. The co-existence of both species in the field is presumably due to the variable host preference of *Habrocytus trypetae*. The preference for the gall-fly is partly overcome when suitable hosts are scarce, as in May 1935.

This application of Nicholson & Bailey's theory to the study of the steady state has produced a series of calculated values for the population densities of the gall-fly and of *Eurytoma curta* which agree closely with the values found in the census. This result has been achieved by the substitution in the formulae of values estimated from the census data for both the natural rate of increase of the gall-fly, and the area of discovery of *E. curta*. A value for the non-specific mortality has been used which is rather less than that found in the only complete year studied.

By thus combining theory and measurement, two major conclusions have been reached: First, that in the census area the chalcid parasite *E. curta* was the factor primarily responsible for the control of the

population density of the knapweed gall-fly, although it caused only a small proportion of the whole mortality. Secondly, that most of the remaining mortality factors, which together destroyed the greater proportion of the gall-flies, had the long-term effect of increasing the average population density of the gall-fly. This was because they killed *E. curta* and the gall-fly indiscriminately, and hence reduced the efficiency of *E. curta* as a controlling agent.

Up till now consideration has been given only to the steady state. In nature the steady state is not realized because environmental conditions are not steady, and affect the balance in various ways. Thus the weather influenced the behaviour of the gall-flies, and probably altered their fecundity. Temporary summer flooding killed many gall-fly larvae and some of the parasites. The weather in the early spring and summer greatly altered the times of emergence of *Habrocytus trypetae* in relation to the availability of gall-fly larvae or pupae suitable for parasitization. The fraction of flower-heads which fell to the ground differed in different winters, thus varying the fraction of larvae subjected to winter disappearance and destruction by mice. Changes of these kinds at times favour the gall-fly, while at other times one or more of the parasites may find conditions particularly suitable. This will result in more or less irregular changes in the population densities of the various species.

The theories of Nicholson & Bailey, of Lotka, and of Volterra suggest that any disturbance of the steady state will lead to periodic oscillations in the population density of host and parasite. Calculation shows that in the gall-fly such oscillations should have a periodicity of a little over 4 years (Nicholson & Bailey, 1935, p. 585). Opinions differ as to whether, under constant conditions, such oscillations are damped (Lotka), or are of constant amplitude (Volterra), or increase in amplitude (Nicholson & Bailey). But unless the primary assumptions of these theories are known to be exact, such long-term predictions are of little objective value. Besides, it can be shown with Nicholson & Bailey's theory that if a proportion of hosts is not available to parasitism, oscillations will be damped instead of increasing in amplitude. Gause (1934) has shown experimentally that oscillations between *Paramecium* and its predator *Didinium* are damped by provision of situations in which *Paramecium* is partly protected from *Didinium*. Perhaps the irregular distribution of the gall-fly larvae in space tends to damp the inherent oscillations between it and *Eurytoma curta*. In those square metres in which there were few gall-fly larvae, the percentage of them parasitized by *E. curta* was below the average (Varley, 1941). However, in a fluctuating environment such oscillations cannot in any case be regular, and the population at any time must be a complex function of the factors operating during the previous years, and cannot be related solely to the conditions of the immediate past.

Schwerdtfeger (1935) gives annual estimates of the population densities of four moths which are pests of the German coniferous forests. Since 1880, when the records begin, all four species have independently shown great peaks of abundance, in which the population density is hundreds or even thousands of times as great as that in the minima in between. In these maxima the trees are largely defoliated. Here intraspecific and interspecific competition for a limited food supply apparently acts as a check to oscillations which might otherwise increase indefinitely in magnitude.

Were there a natural tendency for the oscillations in the population density of the gall-fly to increase in amplitude, the only factor known which could check this increase is the density-dependent early larval mortality. This, as we have seen, would be effective only at very high population densities. But high population densities have not been observed in the field. Preliminary census work in over thirty different localities in England and Wales showed no sample with more than 48 % of the flower-heads containing galls. Eleven samples gave 0%. Eight gave percentages between 1 and 10. Seven were between 10 and 20%, four between 20 and 30%, four between 30 and 40%, and three localities only had between 40 and 48% of the flower-heads galled. The expected period of oscillation is just over 4 years. Of the 26 samples in which the gall-fly was found, perhaps one-quarter represent peaks of population density. This suggests that the peaks of oscillation lead at most to some 40% of the flower-heads being galled, after which the population density falls again.

The observed change in the percentage of galled flower-heads from 44 to 8% in the census area may be interpreted as a glimpse of these oscillations.

Considerable differences have been noted both in the population density and in the specific composition of the population of the knapweed flower-heads at places only a few hundred yards apart. Hence the rate of dispersal of the insects concerned is not sufficiently rapid either to equalize populations, or to synchronize oscillations over these distances. Very possibly the changes in the population density in a large area will be comparable with the changes in level of a choppy sea. Each point may show more or less regular oscillations in level, but the oscillations observed at different points may not be in phase with each other.

To obtain information on these points will require an uninterrupted study of 10 years or more. This present communication, embracing as it does only

2 years of detailed census work, must be regarded as preliminary and incomplete. However, since the work was first broken off in 1937 no opportunity has arisen to continue it on a sufficient scale. The results are therefore presented as they stand in the hope that the methods employed may have wider application in the fields of ecology and economic entomology, and that they may serve to stimulate further intensive studies of this and other animal communities.

Summary

1. A detailed study has been made of the insect community living in the flower-heads of the black knapweed, *Centaurea nemoralis* (Compositae). The problem considered here is: What factors control the population density of the knapweed gall-fly in nature, and how do they operate?

2. A solution is found by the application of Nicholson & Bailey's theory of 'balance of animal populations' to the results of a detailed census of a series of 92 square-metre plots from an area near Cambridge over a period of 2 years.

3. The population density of the gall-flies was estimated to be 6·9 flies per sq.m. in July 1935, and about 2·0 per sq.m. in 1936. The changes in the population density per sq.m. are given in Table 8.

4. The fecundity of the gall-flies was estimated from the census data to have been 70 eggs per female in 1935, and 52 eggs per female in the colder July of 1936. These results are considered in relation to experiments on the effects of mating, nutrition, temperature and humidity on the fecundity of the flies, and in relation to detailed observations of the behaviour of the flies in the field.

5. The cause of the mortality in the eggs and young larvae is discussed. The young larvae form galls in the knapweed florets.

6. Mortality after gall-formation was partly due to the chalcid parasites *Eurytoma curta* and *Habrocytus trypetae*. Subsequent mortality was largely non-specific, and killed these parasites and the remaining gall-fly larvae indiscriminately. These factors, including caterpillars, mice, winter disappearance, other parasites and summer flooding, killed between them 96% of the gall-fly larvae in the 1935–6 generation.

7. The controlling factors which keep a population in balance must be affected in their severity of action by the population density on which they act. Three factors were found to be so affected.

(*a*) The early larval mortality. If this competitive factor had operated alone, a population density of 2400 flies per sq.m. might have been reached.

(*b*) The chalcid parasite *Eurytoma curta*. Its fecundity was reduced by a fall in the population density of the gall-fly larvae. Its area of discovery was estimated to be 0·25 sq.m. Using Nicholson & Bailey's theory, the steady density of gall-flies which it could maintain if it was the only factor operating after gall-formation was calculated to be 0·68 adult gall-flies per sq.m. This is well below the observed figures.

(*c*) The chalcid parasite *Habrocytus trypetae*. This species has two or three generations in the year, and adults emerged at times when few or no suitable hosts were available. This resulted in a great fall in its population density, and prevented it from being an effective controlling factor.

8. The effect of the non-specific mortality, killing as it does an equal fraction of the larvae of the gall-fly and those of *Eurytoma curta*, is to decrease the efficiency of this parasite as a controlling agent. It thus increases the steady density of the gall-flies and their larvae. Using constants derived from the census data, and using a figure of 92% for the non-specific mortality, the calculated steady density of the adult gall-flies is 3·3 per sq.m., and the percentage of parasitism is 31. These figures are intermediate between the observed figures for 1935 and 1936.

9. Combining all the major mortality factors, this theory gives calculated steady densities of host and parasite in good agreement with observed facts. Some reliance may therefore be placed on its analysis of the effects of the different types of factor. All mortality factors do not necessarily tend to reduce the mean populations on which they act.

10. Regular oscillations about the steady state are inherent in the parasite-host relationship. These oscillations may not be of ever-increasing amplitude, as supposed by Nicholson & Bailey, but may in fact be damped if some hosts are less available to parasites than others.

11. In a fluctuating environment the oscillations cannot be regular, and the census data are interpreted as a glimpse of irregular oscillations occurring about the steady state.

12. This use of Nicholson & Bailey's theory supplies for the first time an analysis of the mutual effect of parasitic and other factors of destruction on the population density of an insect. Its possible applications to other problems of insect ecology, and to biological and insecticidal control, are obvious.

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APPENDIX

Table A. *Data from sq.m. samples nos.* 23–46, *collected between* 30 *July and* 22 *October* 1935

	Total no. of flower-heads	No. of flower-heads containing gall-fly eggs or larvae	No. of gall-cells
	342	76	(181)
	375	56	(107)
	430	94	208
	390	112	254
	224	63	172
	236	33	86
	306	54	102
	405	84	191
	200	47	94
	270	61	145
	436	42	99
	332	135	422
	383	130	300
	264	98	267
	133	54	147
	15	6	13
	43	10	23
	207	53	119
	164	68	171
	79	27	68
	88	13	37
	136	31	90
	73	17	36
	225	83	203
Sum	5756	1447	3247
Mean	$\frac{5756}{24}=239{\cdot}83$	$\frac{1447}{24}=60{\cdot}29$	$\frac{3247}{22}=147{\cdot}591$
Sum of squares of deviations	385,193	30,030	213,766
No. of degrees of freedom N	23	23	21
Estimated standard error	26·4	7·37	21·5

Table B. *Data from sq.m. samples nos.* 64–92, *collected between* 28 *July and* 6 *October* 1936

No. of gall-cells given for samples nos. 73–92. Some gall-fly eggs present in samples up to no. 72, collected 14 August.

	Total no. of flower-heads	No. of flower-heads infested by gall-flies	No. of gall-cells
	(176)	20	—
	(102)	6	—
	(59)	0	—
	(106)	5	—
	(132)	7	—
	(201)	3	—
	(178)	28	—
	(230)	21	—
	(156)	21	All galls complete
	103	7 17 Aug.	19
	302	23	53
	228	11	33
	111	10	22
	136	10	19
	139	17	37
	191	7	15
	75	7	15
	319	41	104
	130	21	50
	117	13	28
	131	11	24
	110	7	9
	104	6	12
	130	9	20
	133	10	27
	128	15	40
	52	3	5
	81	6	10
	74	12	20
Sum	2794	357	562
Mean	$\frac{2794}{20}=139{\cdot}7$	$\frac{357}{29}=12{\cdot}31$	$\frac{562}{20}=28{\cdot}1$
Sum of squares of deviations	93,860·2	2,168·21	9,286·2
No. of degrees of freedom N	19	28	19
Estimated standard error	15·7	1·6	4·9

Table C. *Number of gall-cells in the year-old galls found in the summer of* 1936 *in sq.m. samples nos.* 47–82

62	69	11	33
16	43	0	13
62	32	27	29
97	57	22	15
46	76	87	47
23	119	184	28
49	100	12	29
77	72	155	83
74	61	25	119

Σx 2045. $\bar{x}$ 56·8055. Squares of deviations 60,836.
Estimated S.E. 6·96. Mean no. of gall-cells = $56{\cdot}8 \pm 7{\cdot}0$.

Table D. *Emergence and fecundity of* Eurytoma curta *in* 1935

The number of *E. curta* found in sq.m. samples nos. 14–21, 23–27 gives directly the number to emerge.

Metre no.	Larvae	Pupae	Emerged	Total
14	2	.	.	2
15	.	.	.	0
16	.	7	.	7
17	.	1	3	4
18	.	.	.	0
19	.	.	.	0
20	.	.	2	2
21	.	.	.	0
23	.	.	5	5
24	.	.	.	0
25	.	.	4	4
26	.	.	2	2
27	.	.	.	0
				26

Mean $26/13 = 2{\cdot}0$. Sum of squares of deviations $= 66$. No. of degrees of freedom $N = 12$. Estimated S.E. $s = 0{\cdot}65$.

The number of eggs laid per sq.m. can be estimated from the total number of available hosts per sq.m. $= 147{\cdot}6 \pm 21{\cdot}5$ minus 3 per sq.m. died of unknown causes, leaving 144·6, and the fraction of these parasitized by *Eurytoma curta*.

The fraction parasitized was estimated only from those hosts in which the presence or absence of *E. curta* could be ascertained. The figures were: 1131 *E. curta* observed in 2479 hosts, giving a fraction parasitized $= 0{\cdot}457 \pm 0{\cdot}010$.

The number of eggs laid per sq.m.

$$= 144{\cdot}6 \times 0{\cdot}457 = 66 \pm 10.$$

The proportion of females was estimated at $0{\cdot}52 \pm 0{\cdot}05$.

The number of eggs laid per female

$$= 66/(2{\cdot}0 \times 0{\cdot}52) = 63 \pm 23.$$

Table E. *Emergence and fecundity of* Eurytoma curta *in* 1936

The number of *E. curta* found in the year-old galls in the summer of 1936 in sq.m. samples nos. 47–82, excluding those killed by factors operating in 1935.

10	3	0	1
1	1	0	0
2	1	4	5
3	3	4	0
1	14	11	3
3	15	8	1
0	8	3	1
2	7	15	9
0	2	2	16
			159

Mean $159/36 = 4{\cdot}42$. Sum of squares of deviations $= 811$. No. of degrees of freedom $N = 35$. Estimated S.E. $s = 0{\cdot}80$.

Effectively emergence had ceased by the end of July. Sq.m. samples nos. 67–82 examined after July showed that out of 85 *Eurytoma* which had survived the winter, 32 had emerged. The fraction of emergence $32/85 = 0{\cdot}377 \pm 0{\cdot}053$.

Combining these figures, the number of *E. curta* which emerged per sq.m. $= 4{\cdot}42 \times 0{\cdot}377 = 1{\cdot}66 \pm 0{\cdot}38$.

The number of eggs laid per sq.m. can be estimated from the total number of available hosts per sq.m. $= 28{\cdot}0 \pm 4{\cdot}9$ minus $1{\cdot}2 \pm 0{\cdot}4$ per sq.m. which died, leaving $26{\cdot}8 \pm 4{\cdot}9$ hosts per sq.m.

The fraction of available hosts parasitized was

$$107/396 = 0{\cdot}270 \pm 0{\cdot}022.$$

The number of eggs laid by *E. curta* per sq.m. is given by $26{\cdot}8 \times 0{\cdot}270 = 7{\cdot}2 \pm 1{\cdot}4$.

Since the proportion of females is $0{\cdot}52 \pm 0{\cdot}05$, the number of eggs laid per female

$$= 7{\cdot}2/(1{\cdot}66 \times 0{\cdot}52) = 8{\cdot}4 \pm 2{\cdot}6.$$

Table F. *Frequency distribution of live and dead gall-fly eggs in* 1935

No. of eggs in flower-head	No. of live eggs													Total no. of flower-heads
	0	1	2	3	4	5	6	7	8	9	10	11	12	
1	3	26	.	.	.	.	.	.	.	.	.	.	.	29
2	1	5	32	.	.	.	.	.	.	.	.	.	.	38
3	0	1	6	29	.	.	.	.	.	.	.	.	.	36
4	0	0	1	4	18	.	.	.	.	.	.	.	.	23
5	0	0	0	0	1	7	.	.	.	.	.	.	.	8
6	0	0	0	0	1	0	4	.	.	.	.	.	.	5
7	0	0	0	0	1	0	1	3	.	.	.	.	.	5
8	0	0	0	0	0	0	0	0	2	.	.	.	.	2
9	1	0	0	0	0	0	0	0	0	0	.	.	.	1
10	0	0	0	0	0	0	0	0	0	0	0	.	.	0
11	0	0	0	0	0	0	0	0	0	0	0	0	.	0
12	0	0	0	0	0	0	0	0	0	0	0	0	1	1

Dead eggs $40/447 = 0{\cdot}089$.

Table G. *Frequency distribution of live and dead gall-fly eggs in* 1936

No. of eggs in flower-head	No. of live eggs										Total no. of flower-heads
	0	1	2	3	4	5	6	7	8	9	
1	6	16	.	.	.	.	.	.	.	.	22
2	3	0	15	.	.	.	.	.	.	.	18
3	2	3	2	11	.	.	.	.	.	.	18
4	0	1	0	1	9	.	.	.	.	.	11
5	1	0	0	0	2	6	.	.	.	.	9
6	0	0	0	0	1	1	4	.	.	.	6
7	0	0	0	0	0	0	1	2	.	.	3
8	0	0	0	0	0	0	0	0	0	.	0
9	0	0	0	0	0	0	0	0	0	1	1

Dead eggs 41/267 = 0·153.

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THE DETERMINATION OF THE AGE AND GROWTH OF THE PERCH (*PERCA FLUVIATILIS*) FROM THE OPERCULAR BONE

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(With Plate 4, and 6 Figures in the Text)

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1. INTRODUCTION

The fact that many fish show rings on such skeletal structures as scales, bones, otoliths and fin rays, has been known for a long time. In many cases these rings have been shown to be annual in formation and to be probably due to seasonal fluctuations in growth. They thus provide a very useful method for assessing the ages of fish, and as such have been extensively used by many workers. In fact, age determination, usually from the rings on the scales, has become one of the standard methods in fishery research. Age determinations are very useful in practical fishery management as they can lead to assessments of mortality rates and by calculations of the mean sizes of the age groups to a knowledge of the growth rates of the fish. Additional information on the growth of fish can also be ascertained from the scales and similar skeletal structures by calculating the length of a fish at each year of its life from the proportional width of the rings laid down each year. These methods have been very widely used and a large proportion of the extensive modern research on fish ecology and fishery management is based on age and growth studies using the 'scale method'.

There is also a large literature on the validity of the use of these methods, which discusses whether the rings are true annual formations and whether they provide accurate estimates of past growth. Although there is relatively little substantial direct evidence of the soundness of age and growth determinations from scales, the sum of indirect evidence leaves no doubt that in general their use is justified. At the same time the practice of many workers, who have published accounts of age and growth based on the scale method without attempting to substantiate the validity of its application to the species or problem studied, is to be deprecated. The present paper is a preliminary to an account of the study of perch (*Perca fluviatilis* L.) in Windermere, and its aim is to demonstrate that the methods used to determine age and growth are valid. The literature on the method and the investigations towards proving its correctness has been discussed by several workers, and the papers of Graham (1929) and Van Oosten (1929, 1941) give detailed reviews. It is not intended here to enter into a general discussion on the scale method and its validity.

In the perch, some age and growth studies have been made by Scandinavian and German workers, and recently the ecology of the closely related yellow perch (*P. flavescens* Mitchill) has been investigated in many North American waters. In nearly all cases the scales have been used, but Nilsson (1921) concluded that in practice the opercular bone was more accurate and easier to use than the scales. Roper (1936) used scales and operculars in a study of perch in Germany, and found that infra-red photography helped to reveal the obscure inner annual rings on the operculars. The opercular bone has also been used by Nikolsky & Evtiukhov (1940) to determine the age of *P. shrenki* Kessler. Segerstrale (1933) has studied the use of the scales of the perch in detail, has shown the need for correcting back-calculated readings of growth made by direct proportion, and has constructed a curve for this purpose.

When data were collected from the perch in Windermere in connexion with the current trap fishery experiment (Worthington, 1941), Mr H. J. Buchanan-Wollaston tried using the opercular bones and compared them with scales from various parts of the perch. He discovered that the use of polarized light often clarified the rings on the operculars, and that by projection the width of these rings could easily be measured. He found that in general the

operculars of the Windermere fish were easier to read than the scales, although at times it was useful to examine both.

The purpose of the present paper is (1) to describe the opercular bone of the perch and to give an account of the methods of examining the rings which it shows; (2) to demonstrate that these rings are true annual formations; (3) to show that there is a constant relationship between the growth of the opercular and the growth of the fish, and that the length of a fish at each year of its life can thus be calculated from the width of the rings on the opercular; and (4) to put forward evidence that the lengths so estimated are reasonably accurate. It does not attempt an analysis of the structure or growth of the opercular nor of the factors causing the seasonal rings on that bone. Nearly all the data used were collected and analysed primarily for other studies and have only been used for this paper in so far as they provide information on the method of age and growth determination and its accuracy.

2. THE COLLECTION OF DATA

This paper is devoted entirely to operculars from Windermere fish, but it appears from examination of a few perch from other waters in the Lake District, from Loch Lomond, and from three places in the south of England, that the operculars are similar on perch from other British localities. The fish were collected by various fishing methods including wire-netting traps, seines, gill nets, a young fish trawl, long lines, and angling. Measurements of length were all made from the anterior tip of the pre-maxilla to the distal end of the longest caudal fin ray (see Fig. 1). They were nearly all recorded in 0·5 cm. groups designated by the lower limit as is customary in fishery research; thus to turn these recorded lengths into actual lengths 0·25 cm. has to be added to the means of samples. The fish were classified into age groups according to the number of completed years of life, and the beginning of June, after the end of the spring trapping season has been taken as the date of hatching for this purpose.

When large samples were caught all the fish in the catch, or in a random sample, were measured by 'pricking' their lengths on to waxed paper ruled in 0·5 cm.; and a smaller sample of operculars was taken, representative of the various sizes of fish. In small samples usually all the operculars were collected. Male and female fish of over 8·0 to 10·0 cm. were treated separately as there are considerable differences between the growth rates and other features of mature fish of the two sexes. In general, the left-hand opercular only has been collected, although occasionally both were taken.

The opercular was easily and rapidly removed from the fish by slipping the point of a scalpel under the posterior edge of the bone between the opercular and the sub-opercular, as shown in Fig. 1. The scalpel was then moved ventrally until it reached the ventral end of the opercular when it was twisted so as to lift up the opercular. The bone was then gripped

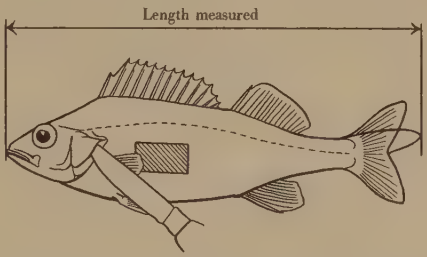


Fig. 1. Diagram of a perch to show (1) method of measurement, (2) method of removing the opercular, and (3) region from which scales were taken (the shaded rectangle).

between the fingers and with a twist pulled away from its point of articulation with the skull. Once it had been discovered during the early stages of the work that the operculars were more suitable, usually no scales were taken from samples of fish. Sometimes, however, a few were collected for comparison with the operculars, in which case they were removed from the side of the fish, below the lateral line, and opposite the distal end of the pectoral fin (Fig. 1).

3. THE READING OF AGE AND GROWTH

The operculars were prepared by soaking them for a short while in cold water and then dipping them into boiling water. After this treatment they could easily be cleaned with a cloth between the fingers. The rings then showed up quite clearly when the bone was dry. Cleaning was most easily done soon after the operculars had been collected. Once they had been cleaned, however, keeping tended to improve the clarity of the annual rings.

For examination of the operculars, a simple projector was used to throw an image of the bone vertically upwards on to a sheet of ground glass about 10 cm. square. The bones were thus magnified about five times. Light was polarized by placing a 'Polaroid' glass disk between the projector's condenser and the opercular. Another polarizing disk was placed on top of the projector. Both disks and the opercular could be rotated independently of one another, and the operculars were usually examined with several different lightings and arrangements of the polarizers. When the age of the bone had been decided upon, the position of the 'centre', the winter rings, and the edge were marked off on a narrow strip of tracing paper; the straight edge of this paper being

placed along a line passing through the 'centre' of the bone and perpendicular to its posterior edge. The paper was then placed on a sheet of accurate squared paper and adjusted so that the centre mark was at the origin, and the edge mark opposite the recorded length of the fish on the ordinate scale. The respective proportionate lengths were then read off on the same scale, opposite the marks representing successive winter bands. These readings, like those of the final lengths of the fish, were made in terms of 0·5 cm. length groups.

On the opercular bone (Pl. 4) broad, opaque zones correspond to the rapid growth of the summer, and each of these gradually fades into a narrow transparent winter zone, which ends relatively abruptly, with a sharp line of discontinuity between it and the next summer zone. This sharp line marking the end of the winter band was always taken as the end of the year's growth. In well-dried operculars the rings show up most clearly when viewed with reflected light against a dark background. This kind of lighting shows the transparent winter zones dark and the opaque summer zones white, and is also the best lighting for distinguishing between true and false rings. For measurement of the rings, however, transmitted light was used and in this case the rings showed up clearest with polarized light and when the two 'Polaroid' disks were crossed. Different appearances were given to the rings by different settings of the disks and by the rotation of the opercular between them. In many of the bones the innermost, or first, winter ring was more a change over from one broad zone to another, it was often not clear without the use of the polarizers, and even then it was generally difficult to place in large and thick operculars. Most of the growth of the perch in Windermere is confined to the months between May and October and operculars from fish caught between October and April showed the beginning of a transparent 'winter' band on the edge. The abrupt ending of the winter ring, its really characteristic feature, could not, however, be seen on the edge of the opercular till the perch had started its next season's growth. Apart from the different character of the first winter ring no obvious differences were found between the rings laid down when the fish were immature and when they had spawned, comparable to the spawning marks on the scales of the Salmonidae.

The gradual change from opacity to transparency ending abruptly at the beginning of another opaque zone is characteristic of the true annual ring, and although false rings were sometimes frequent, on careful examination they could usually be distinguished by their abrupt change from an opaque zone to a thin transparent band followed again by an opaque zone. In one case the formation of a false ring on the operculars of nearly all the fish from one locality was traced by a succession of samples throughout the summer. Although, when it first appeared, this ring was sometimes mistaken for a true annual ring, when new summer growth had been added outside it, its false nature was realized and the mistakes corrected. The false rings were usually found in the middle of the summer's growth, and in fast-growing fish there is often a rather sudden reduction in opacity half-way through the summer zone which was sometimes on first examination mistaken for an annual ring. Although with young and fast-growing fish there was rarely any doubt as to the age, in some older fish several different interpretations could be made. After practice it was possible to give nearly all of these an estimated age, though in many cases more by the general appearance of the rings, than by any definable characters.

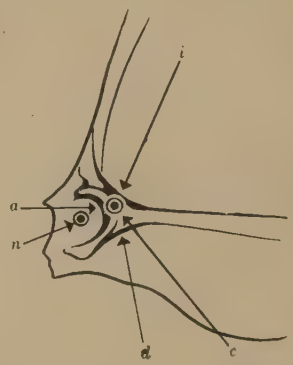


Fig. 2. Diagram of the central region of an opercular showing the centres, a = centre of anterior face; c = centre used in back-calculation; d = centre of dorsal face; i = centre of internal face; n = centre used by Nilsson.

There was some initial difficulty in deciding which was the correct centre of growth of the opercular. However, on examination the bone appeared to consist of four 'faces': (1) an exterior which was somewhat convex, (2) a posterior, the rings on which were used to measure growth, (3) a dorsal, and (4) an anterior, which articulated with the skull. Each of these bore annual rings, centred round a small hole. The centre, or origin of growth, was taken to be the point, in the thickest region of the bone, where the holes appeared to meet. This point was not definitely marked on projected bones, but its position could be judged with adequate accuracy. This practice is different from that of Nilsson (1921), who used as the origin the mid-point of the circular anterior face (Fig. 2).

Very occasionally scales were examined to check the reading of age given by the opercular. In general, these gave an identical number of annual rings, but false rings seemed to be more prevalent on scales than

on the operculars, though their presence often corresponded in the two cases. No detailed study of the scales has been made, and only the opercular of most fish was used. The scales of the perch have been studied in some detail by Segerstrale (1933).

4. THE ACCURACY OF THE AGE DETERMINATIONS

The accuracy of age determinations made from rings on scales or bones can be substantiated by evidence of at least five main kinds (Graham, 1929; Van Oosten, 1929, 1941):

(1) In length-frequency curves of young fish, each age group is generally represented by a distinct mode. Agreement between the age as determined from the successive modes and as determined from the number of rings on the skeletal structure is evidence of the accuracy of the latter. Substantial agreement between the modal lengths of frequency curves and the mean lengths as back-calculated by a correct method from the rings on scales or bones is additional evidence of this type.

(2) In a population of fish, variations in the success of the annual hatch may lead to considerable variations in the relative abundance of the year classes. This may make a particular year class recognizable as unusually abundant or scarce, and so through its annual appearance as a successively older age group each year, a check can be made on the annual formation of the rings on skeletal structures.

(3) If the rings on the scales or bones are annual formations, examination of their growing edge throughout the year should reveal an annual cycle in the structure seen at that edge.

(4) Fish can be marked when fry, or at a known age, and then released. When recaptured the number of rings on their skeletal structures should agree with their known age.

(5) Fish reared in ponds or aquaria are often of known age, and the rings on their scales and bones can be checked against this known age.

The main evidence produced in support of the rings on the perch opercular being annual formations falls into the first three of the catagories given above. The length frequencies of younger perch are presented first in some detail, and then an example is given of a dominant year class being traced in two successive seasons. The appearance of the edge of the opercular throughout the year has not been analysed, but mention has already been made that operculars of fish caught in the summer invariably showed 'plus growth' outside a completed winter ring.

Samples of small perch caught at different times of the year have been measured and all the length-frequency data thus obtained are summarized in Table 1, and shown as histograms in Fig. 3. The samples were obtained by different methods of capture, each selective of a different size range of fish. There was not always a very adequate series of samples available and in the data for a few of the months some age groups are represented by only one or two small samples obtained by methods somewhat selective of the larger individuals, and often separated by a long period of growth. As the samples were taken from different stations in the lake, and over a period of 5 years, fish with slightly different growth rates have been included in the data, and thus have tended to increase the variance of size in each age group and to make the length-frequency distributions flatter than normal.

Fig. 3 shows however that the perch below 12·5 cm. in length consisted of three age groups, which may be designated the O, I, and II groups. The O group hatched in May and June and had grown by the end of the summer to about 5·5 cm., at which size it passed the winter. On becoming 1 year old, and thus the I group, these fish then commenced rapid growth again, reaching about 11·0 cm. by the end of the growing season. In their third year of life they increased to over 13·0 cm.

Individuals taken from the O group showed no 'winter ring' on their operculars until after the first winter, and examples of the I group caught in the summer showed one winter ring inside a band of summer growth; and the II group fish likewise had two winter rings. The modes of the length-frequency curves of young fish thus corroborate the readings of annual rings on the operculars.

The length-frequency distribution of a trapped sample of fish over 9·0 cm. in length and caught in May is tabulated in Table 2 and graphed in Fig. 4. A sample of operculars was taken off the fish of each length group in this catch, and the operculars in each of these samples classified according to the number of their winter rings. The classification of these operculars into age groups is also given in Table 2 and Fig. 4. It will be seen that there are two principal modes in the length-frequency distribution corresponding to fish with operculars bearing two winter rings, and those with three and four winter rings. The latter mode has a compound appearance especially in the case of the female fish. The few larger fish had operculars with often more than four winter rings. The mode at 11·0 cm., from the evidence both of the length-frequency distributions and of the operculars, is thus shown to be constituted of I group fish (when they are nearly 2 years old), and the ages of the larger fish given by the operculars do not conflict with the most probable analysis of the length-frequency distributions of these fish.

It was found after several years' sampling that there was considerable variation in the numerical abundance of fish hatched in different years. Fish of

one year class frequently showed a preponderance over those a year younger and those a year older. One example of this is given in Table 3 which shows the age distribution as deduced from opercular readings, of two comparable samples taken in the same month at the same place, but the second a year after the first. A majority of the fish (57 %) in the 1944 sample had four rings on their operculars, indicating that they belonged to the 1940-year class and were 4+ years old; while a majority (71 %) of the 1945 sample had

grew in direct proportion to the fish. The lengths at each year were calculated from the formula:

$$Fx = Fy\frac{Bx}{By},$$

where Bx = length (or diameter, etc.) of the scale or bone at a particular age, Fx = the corresponding length of the fish, By = final length of the scale, and Fy = final length of the fish. Alternatively, the lengths could be read off a projected image of the scale or

Table 1. *Monthly length frequencies of perch below 13·0 cm. All samples to 1944 combined. In the spring and autumn totals data, additional to those given under the separate months, have been added; the exact date of capture of these fish is unknown*

Length group (cm.)	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.–Apr. (+others)	Oct.–Dec. (+others)
0·0–	—	—	—	—	—	—	—	—	—	—	—	—	—	—
0·5–	—	—	—	—	100	67	—	—	—	—	—	—	—	—
1·0–	—	—	—	—	—	186	12	—	—	—	—	—	—	—
1·5–	—	—	—	—	—	18	172	2	—	—	—	—	—	—
2·0–	—	—	—	—	—	—	323	69	—	—	—	—	—	—
2·5–	—	—	—	—	—	—	339	221	6	—	—	—	—	—
3·0–	—	—	—	—	—	—	141	281	26	—	—	—	—	—
3·5–	—	—	—	7	1	—	5	302	132	15	—	—	7	15
4·0–	1	—	—	44	26	—	—	305	416	67	—	4	45	71
4·5–	8	—	3	275	112	—	—	104	718	130	—	7	286	137
5·0–	20	—	11	553	221	2	1	14	789	74	—	15	584	89
5·5–	31	1	31	585	206	4	—	—	672	35	12	8	648	55
6·0–	33	1	13	333	102	19	1	2	325	10	8	2	380	20
6·5–	19	1	—	122	36	39	—	6	143	6	20	—	143	26
7·0–	9	—	1	29	8	102	9	5	38	—	18	—	39	18
7·5–	7	—	—	3	4	162	28	37	1	—	4	—	10	4
8·0–	1	—	—	—	2	174	88	164	1	—	3	—	1	3
8·5–	—	—	—	—	—	146	144	429	2	—	—	—	—	—
9·0–	—	—	—	—	4	71	114	616	15	4	—	—	—	4
9·5–	1	—	—	—	46	30	82	666	25	3	—	—	3	3
10·0–	—	1	1	7	186	4	36	413	22	9	—	—	12	13
10·5–	—	—	1	20	442	1	15	273	31	20	—	3	30	26
11·0–	1	1	3	27	530	3	23	144	15	15	—	1	54	22
11·5–	—	—	2	26	326	2	43	73	14	3	—	2	43	7
12·0–	—	—	—	17	227	3	34	101	12	5	—	1	30	14
12·5–	—	1	1	15	315	4	23	119	20	6	—	—	29	12
Total	131	6	67	2063	2894	1037	1633	4346	3423	402	65	43	2344	539

five rings on their operculars, thus indicating that they were the same year class as that dominant in 1944, but were a year older, and had added one ring to their operculars during the intervening winter. This can be considered as additional evidence that the rings on the operculars are annual rings and are thus accurate indications of age.

5. THE BACK-CALCULATION OF GROWTH

When growth made in each year of life has been back-calculated from the rings on the scales or bones of fish it has often been assumed that the scale or bone

bone by a graphical method such as the one described above for the opercular of the perch. This method of back-calculating the growth of a fish is often known as the 'Dahl-Lea' method, after its principal originators.

The method has been used very widely, often without its accuracy being questioned, but in many cases when the method has been tested by comparing the mean lengths of age groups as measured from actual fish and as back-calculated from older fish inaccuracies have been discovered. In some cases they were not large enough to be of practical importance, but in other cases they were large and consistent

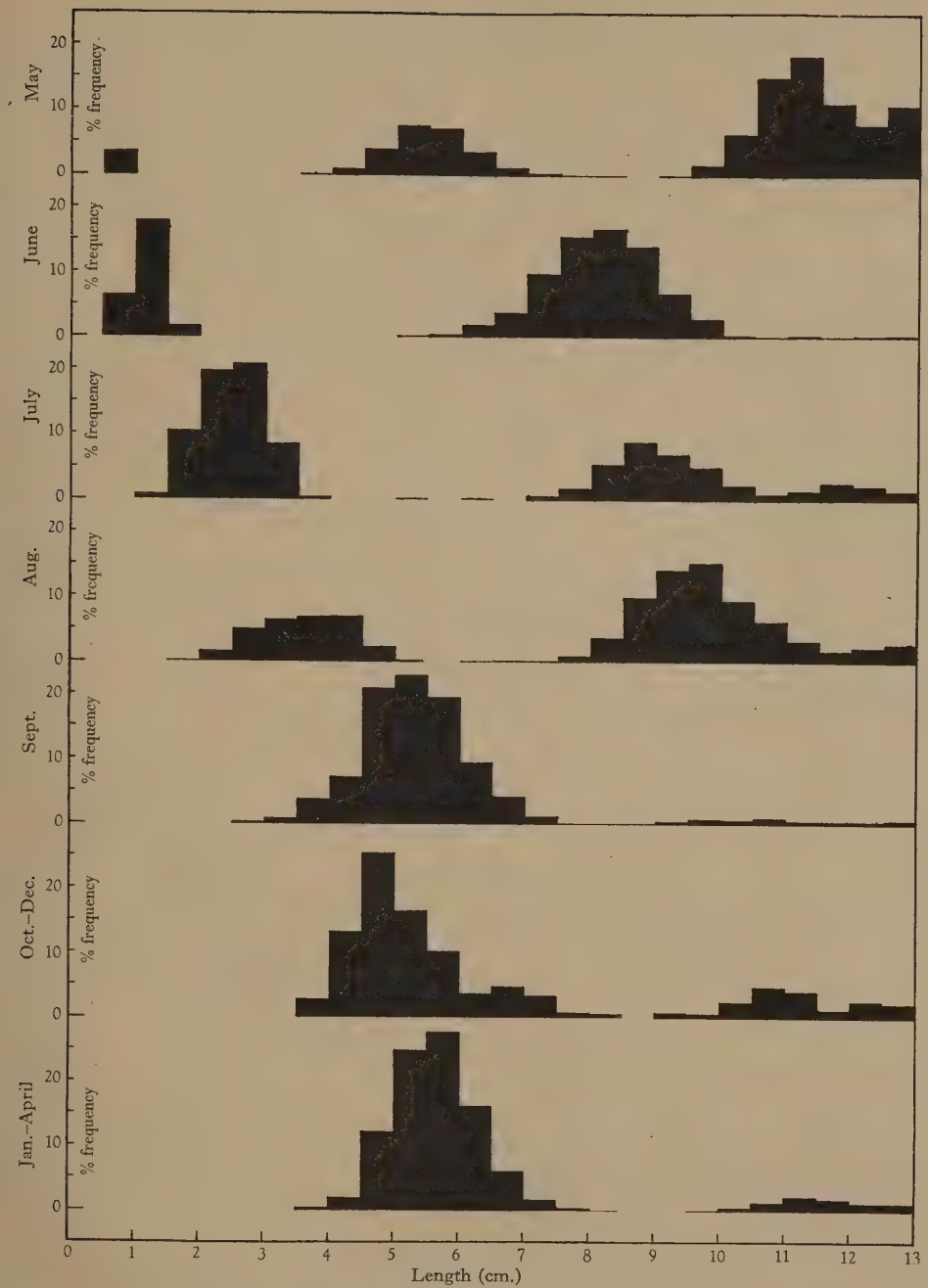


Fig. 3. Length frequencies of small perch for each summer month, autumn and spring.

enough to be impossible to ignore. The causes of these inaccuracies have not in every case been proved, but they are usually of two types: (1) the scale or bone and the fish do not grow in direct proportion to one another, growth is *allometric* rather than *isometric*, or (2) selective sampling or differential mortality causes the mean length of those individuals in a population cannot readily be made for causes of type (2), and in fact their discovery may in itself provide important biological information.

Nilsson (1921) compared the results of back-calculating the growth of six male perch from the scales, with those from the operculars, and concluded that there was little significant difference. Also,

Table 2. *Length frequencies of fish caught in a series of fishery traps in* 1944, *and relation to number of winter rings on operculars*

	Males								Females							
Length group (cm.)	Length frequency	Winter rings on operculars 2	3	4	5	6	8	Total	Length frequency	Winter rings on operculars 2	3	4	5	6	7	Total
9·0–	1	1	—	—	—	—	—	1	—	—	—	—	—	—	—	
9·5–	19	8	—	—	—	—	—	8	3	1	—	—	—	—	—	1
10·0–	149	26	—	—	—	—	—	26	8	2	—	—	—	—	—	2
10·5–	323	21	—	—	—	—	—	21	29	16	—	—	—	—	—	16
11·0–	419	20	2	—	—	—	—	22	25	9	—	—	—	—	—	9
11·5–	270	15	6	—	—	—	—	21	15	11	1	—	—	—	—	12
12·0–	193	9	19	—	—	—	—	28	20	2	7	—	—	—	—	9
12·5–	267	1	15	—	—	—	—	16	23	1	15	1	—	—	—	17
13·0–	356	—	17	—	—	—	—	17	54	—	19	1	—	—	—	20
13·5–	355	—	22	2	—	—	—	24	85	—	23	4	—	—	—	27
14·0–	208	—	12	4	—	—	—	16	137	—	19	7	2	—	—	28
14·5–	98	—	11	6	—	—	—	17	213	—	18	23	2	—	—	43
15·0–	50	—	6	6	—	1	—	13	224	—	9	22	4	—	—	35
15·5–	23	—	7	9	1	—	—	17	197	—	1	18	1	—	—	20
16·0–	9	—	2	5	1	1	—	9	156	—	2	17	6	1	—	26
16·5–	6	—	1	—	3	—	1	5	86	—	2	16	5	—	—	23
17·0–	3	—	—	1	1	—	—	2	40	—	1	7	10	1	—	19
17·5–	1	—	—	—	—	—	1	1	17	—	—	5	3	—	1	9
18·0–	1	—	—	—	—	1	—	1	8	—	—	1	6	1	—	8
18·5–	1	—	—	1	—	—	—	1	3	—	—	1	1	1	—	3
19·0–	—	—	—	—	—	—	—	—	2	—	—	—	1	—	1	2
19·5–	—	—	—	—	—	—	—	—	3	—	—	—	1	—	2	3
20·0–	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
20·5–	—	—	—	—	—	—	—	—	2	—	—	2	—	—	—	2
Total	2752	101	120	34	6	3	2	266	1350	42	117	125	42	4	4	334

Table 3. *Percentage age distribution* (*age groups I–XI*) *from opercular readings of two samples of perch angled in October at one station in* 1944 *and* 1945. (*All females, the one male caught in* 1944 *omitted*)

Year	Total number of fish	I	II	III	IV	V	VI	VII	VIII	IX	X	XI
1944	124	0·8	0·0	12·1	57·2	21·0	6·5	0·0	0·8	0·0	0·8	0·8
1945	95	0·0	0·0	0·0	14·7	71·6	11·6	2·1	0·0	0·0	0·0	0·0

of young fish that will survive to an old age to be different from the mean length of the whole population. Causes of type (1) are readily discovered and corrected by finding the true proportional relationship between the scale or bone and the fish throughout their growth. This can be done by plotting measured lengths of scales or bones against the corresponding measurements of fish length and finding a suitable line to fit the points. Corrections while admitting that in both cases the growth of the fish was probably not directly proportional to that of the scale or opercular, he thought that the errors involved in assuming that it was would probably be insignificant.

As stated in a previous section, the lengths of the perch at various ages were recorded as read off the operculars by direct proportion. Until the proportionality of growth could be tested it was assumed for

working purposes that either there was an isometric relationship between opercular and fish length or that these back-calculations made by assuming directly

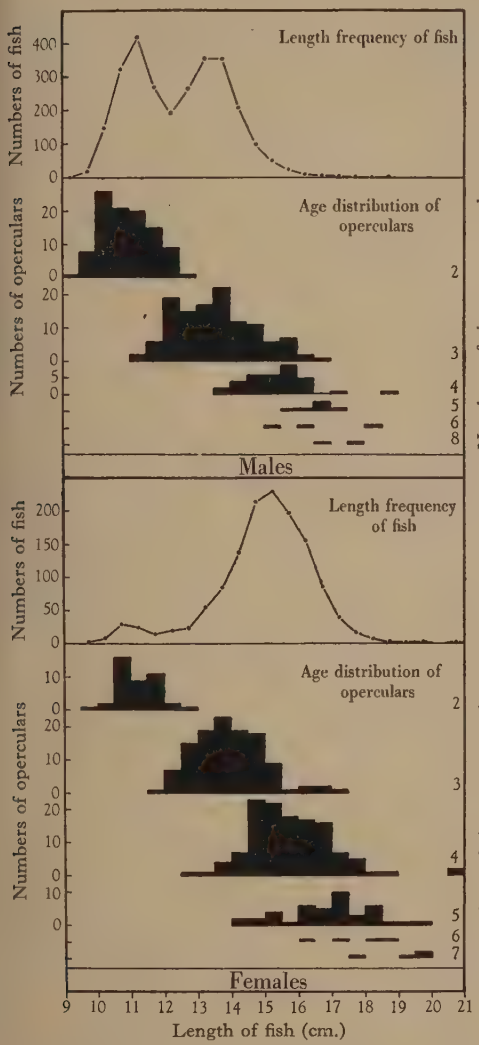


Fig. 4. Length frequencies (*a*) of all fish from a series of traps in 1944, and (*b*) of smaller samples classified into age groups according to the number of winter rings on their operculars.

proportional growth could readily be corrected if allometry was later shown to occur. When sufficient operculars had been collected, however, it was decided to test the proportionality of growth by comparing the lengths of fish and opercular throughout the life of the perch. The bones were measured from the centre to the posterior edge, along a line approximately perpendicular to that edge. The measurements were made to an accuracy of 0·1 mm.; a pair of dividers and vernier were used for all fish 8·0 cm. and over, and an eye-piece micrometer for smaller fish. In fish over 8·0 cm. the measurements for fish of each sex were kept separate. Where possible, operculars from 20 to 30 fish of each sex in each 0·5 cm. length group were measured, and the mean opercular length found for each of these length groups. Above 21·0 cm. the numbers in each length group were small, and above 28·0 cm. only single specimens were available. These mean opercular lengths are given in Table 4.

When these mean opercular lengths were plotted against mean fish lengths it was clear that the points lay along a slight curve and not on a straight line. On the advice of Mr Buchanan-Wollaston this was further tested by plotting, in the form of a dot diagram, the logarithm of opercular length minus the logarithm of fish length against fish length. If the original curve had been due only to the greater variance of the larger fish, these logarithm differences would have formed a broad horizontal band when plotted against fish length as the abscissa. In fact they formed a marked curve. The logarithms of fish lengths were then plotted against the logarithms of the mean opercular lengths, and the points clearly formed a straight line (see Fig. 5). It was then assumed that the lengths of opercular and fish probably obeyed Huxley's formula of allometric growth (Huxley, 1932; Reeve & Huxley, 1945; Richards & Kavanagh, 1945), and accordingly a regression line was fitted to the logarithms of the mean fish lengths upon the logarithms of the mean opercular lengths, for all fish between 8·0 and 21·0 cm. The regression coefficients gave a formula for allometric growth of:

$$\log \text{length of fish} = 1{\cdot}357 + 0{\cdot}9202 \log \text{length of opercular},$$

or $$F = 22{\cdot}76\, B^{0{\cdot}9202},$$

where F = length of fish, and B = length of opercular.

In this formula the figure 0·9202 represents the slope of the regression line, and the ratio between the logarithmic growth rates of the fish and the opercular. It was originally termed the *constant differential growth-ratio* by Huxley (1932), and is now known variously as the *growth constant*, *equilibrium constant* or *growth ratio*. The last term, *growth ratio*, is used here.

It will be seen from Fig. 5 that there is no obvious difference between the values for males and females, and that there is no evidence for a change in the growth ratio at maturity or any other time during the period

Table 4. *Mean length of opercular in relation to length of fish*

Length group (cm.)	Both sexes No.	Mean length (mm.)	S.D.
1·5–	29	0·75	0·07
2·0–	31	0·91	0·09
2·5–	38	1·20	0·10
3·0–	35	1·39	0·11
3·5–	31	1·80	0·10
4·0–	33	2·00	0·14
4·5–	30	2·16	0·12
5·0–	30	2·31	0·14
5·5–	30	2·51	0·14
6·0–	30	2·77	0·18
6·5–	21	3·03	0·13
7·0–	14	3·45	0·32
7·5–	21	3·92	0·16

Length group (cm.)	Males No.	Mean length (mm.)	S.D.	Females No.	Mean length (mm.)	S.D.	Length group (cm.)	Males No.	Mean length (mm.)	S.D.	Females No.	Mean length (mm.)	S.D
8·0–	28	4·23	0·25	23	4·11	0·24	21·5–	1	11·4	—	10	11·66	0·60
8·5–	30	4·55	0·28	30	4·38	0·23	22·0	—	—	—	7	12·00	0·44
9·0–	31	4·69	0·22	27	4·68	0·21	22·5	—	—	—	7	12·21	0·45
9·5–	33	4·90	0·23	28	4·93	0·23	23·0	—	—	—	6	12·48	0·66
10·0–	25	5·06	0·22	21	5·04	0·30	23·5	—	—	—	2	13·30	0·00
10·5–	21	5·26	0·23	24	5·30	0·26	24·0	1	12·6	—	5	12·98	0·38
11·0 -	22	5·57	0·23	21	5·63	0·29	24·5	—	—	—	6	13·50	0·67
11·5–	21	5·78	0·24	20	5·93	0·34	25·0	—	—	—	2	14·20	0·50
12·0–	28	6·19	0·35	20	6·15	0·26	25·5	—	—	—	1	14·0	—
12·5–	20	6·40	0·29	23	6·34	0·27	26·5	—	—	—	2	14·80	0·20
13·0–	20	6·74	0·25	20	6·85	0·31	27·5	—	—	—	3	15·30	0·29
13·5–	24	7·05	0·29	27	7·04	0·34	28·5	—	—	—	1	16·4	—
14·0–	20	7·42	0·24	28	7·12	0·38	29·0	—	—	—	1	15·3	—
14·5–	20	7·98	0·29	41	7·58	0·30	29·5	—	—	—	1	15·5	—
15·0–	20	8·00	0·41	35	8·11	0·36	33·0	—	—	—	1	19·1	—
15·5–	20	8·24	0·30	20	8·31	0·47	34·0	—	—	—	1	19·7	—
16·0–	20	8·46	0·50	26	8·58	0·36	35·0	—	—	—	1	20·8	—
16·5–	20	8·77	0·36	23	8·77	0·44	35·5	—	—	—	1	21·4	—
17·0–	15	9·15	0·42	22	9·19	0·51	36·0	1	22·6	—	—	—	—
17·5–	11	9·33	0·60	21	9·31	0·50	37·5	—	—	—	1	24·0	—
18·0–	7	10·04	0·46	22	9·75	0·26	38·0	1	24·5	—	1	22·2	—
18·5–	7	9·94	0·43	21	9·89	0·48	39·5	1	23·6	—	1	22·9	—
19·0–	2	10·30	0·00	21	9·94	0·51	40·0	—	—	—	1	24·4	—
19·5–	5	10·82	0·23	20	10·57	0·57	41·5	—	—	—	1	26·2	—
20·0–	2	11·35	0·15	20	10·65	0·61	43·0	—	—	—	1	27·7	—
20·5–	1	10·1	—	26	11·00	0·64	44·0	—	—	—	1	28·6	—
21·0–	—	—	—	18	11·41	0·63							

Total numbers of operculars: Unsexed 373
Males 478
Females 713
Grand total 1564

of growth examined. The points for the largest individuals lie somewhat off the regression line, but they are well within the range of variation shown by the smaller fish. The regression coefficient b of 0·9202 was tested for the significance of its difference from unity. The standard error of $b = 0{\cdot}07987$ and so $t = 7{\cdot}226$ and thus is highly significant. The 5% fiducial limits for b as calculated from s_b are 0·8974–0·9430.

Where F_y = the final length of the fish, and B_y = the final length of the opercular, in the perch then:

$$F_y = 22{\cdot}76\ B_y^{0{\cdot}9202},$$

and similarly where B_x = the length of the opercular at any time, and F_x = the corresponding length of the fish:

$$F_x = 22{\cdot}76\ B_x^{0{\cdot}9202}.$$

By the Dahl-Lea method of direct proportion the length of a fish is back-calculated by the formula:

$$F_x = F_y \frac{B_x}{B_y}.$$

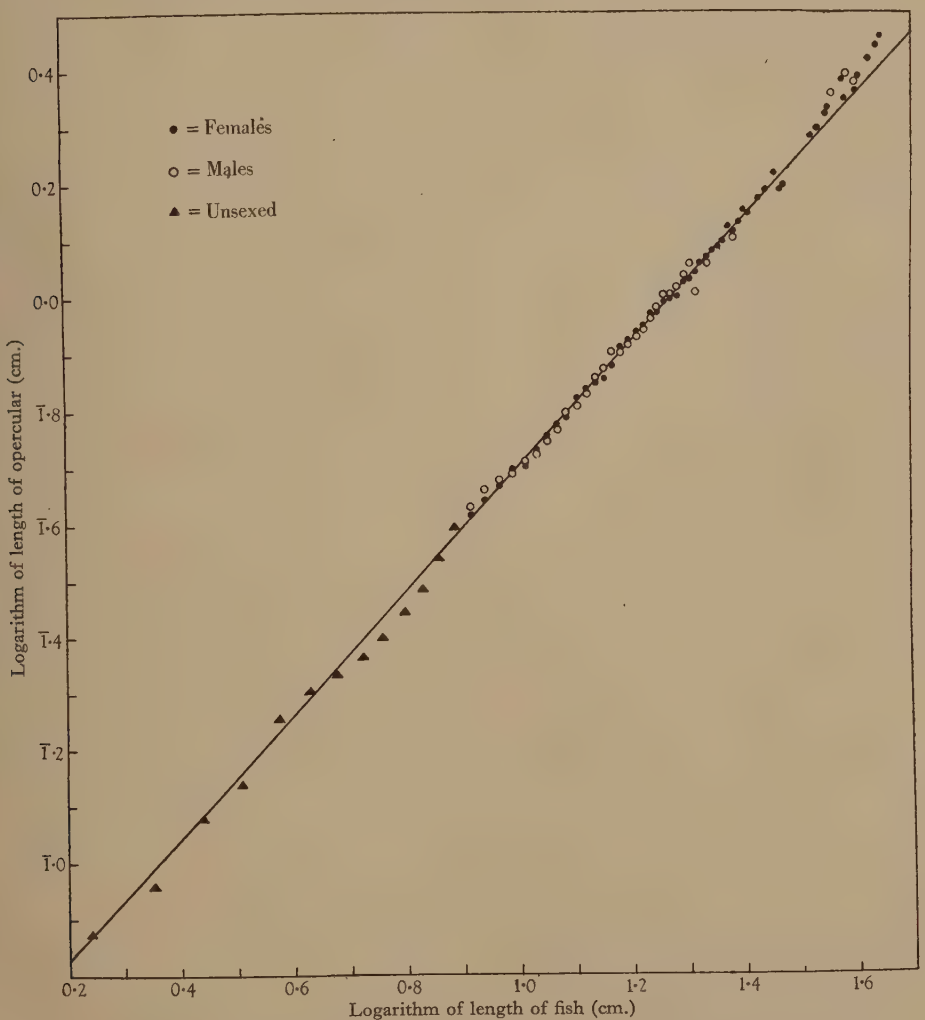


Fig. 5. Logarithm of length of opercular plotted against logarithm of length of fish, with the regression line fitted to the means for fish between 8·0 and 21·0 cm.

But using the opercular of the perch this should become:

$$F_x = F_y \frac{B_x^{0\cdot9202}}{B_y^{0\cdot9202}}.$$

This can also be expressed in a logarithmic form which is easier to compute:

$$\log F_x = \log F_y + 0\cdot9202\ (\log B_x - \log B_y).$$

This formula can be applied to actual measurements of the bone, or to proportions of B_x and B_y, however they may be recorded. Thus if B_x and B_y

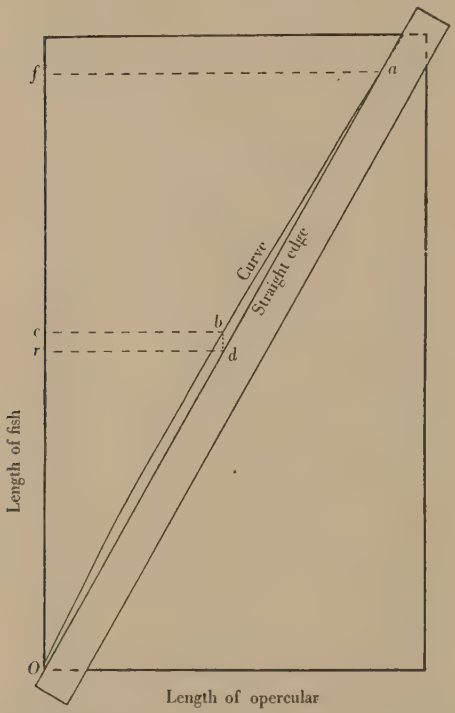


Fig. 6. Diagram showing the method of correcting back-calculations for allometric growth. c = correct back-calculated length, f = final length of fish, r = recorded back-calculated length by direct proportion.

were recorded in terms of directly proportionate lengths of fish, the latter can be corrected for allometric growth by this same formula. This has been done for most of the opercular readings which were originally recorded in the convenient terms of directly proportionate fish lengths.

A quicker way of correction which is sufficiently accurate for individual fish measured only to 0·5 cm. is by means of a graph of the curve of the formula (Fig. 6). If a straight edge is laid from the origin (o) to the point (a) where the curve cuts the final length of the fish (f), the correct reading (c) for any length, will be the ordinate of the point (b) on the curve, which is vertically above the point (d) where the straight edge cuts the horizontal line representing the recorded length (r). In other words, the corrected length differs from the recorded length by the vertical distance between the straight edge and the curve. For practical purposes I have constructed a simple chart with a straight edge fixed to rotate about the origin, and vertical lines drawn from the curve so as to facilitate the making of rapid corrections. The chart is constructed on a scale sufficiently large to give readings in terms of fish length accurate to 1·0 mm.

Any formula when used for back-calculations of growth must assume that in any individual fish there has been an invariable growth ratio, which has probably never been shown. It has been shown, however, that for a number of fish the mean growth ratio is relatively constant, and so there is some justification for assuming the means of back-calculated lengths of a large sample of fish to be reasonably accurate, and it is probably legitimate to use such estimates of growth for single fish, since it is unlikely that there will be any great changes in the individual growth ratio.

Although the growth ratio for the opercular of the perch is 0·9202 and thus nearly 1·0, it would be wrong to ignore the difference. For example, in back-calculating from a fish 20·0 cm. long, a length of 10·0 cm. obtained by direct proportion, should really be 10·6; of 6·0, 6·6; and of 2·0, 2·5. In the last example the difference is as much as 25 %.

6. THE ACCURACY OF THE BACK-CALCULATIONS OF GROWTH

The accuracy of estimates of size back-calculated from the operculars can be tested in at least two ways. The mean lengths of samples of a fish population caught in one year can be compared with the means of back-calculated lengths from samples caught at later dates. Alternatively, records made at different times of the lengths of individual fish, which are marked, or kept in aquaria, can be compared with lengths back-calculated from the operculars when the fish are eventually killed. There is evidence for Windermere perch available from both these sources, and some of the more relevant examples are discussed below.

It is difficult to compare samples of the Windermere perch population taken at different times. First, samples of perch tend to vary in mean size and other characters with the region of the lake from which they come. Thus for comparative purposes samples should come from the same locality. Secondly, most methods of fishing tend to be selective in one way or another so that many catches are not good random samples of the population. Thirdly, over the period of investigation the population has been subjected to

a very heavy and selective mortality by the trap fishery, so that in back-calculating one or more years, not the whole original population is being sampled, but only that part of it which has survived selection by the fishery. As well as this mortality due to the fishery, there is a natural mortality which may well tend to eliminate certain sized individuals. Thus it cannot be expected that samples from the survivors of one or more seasons of fishing and natural mortality will give an accurate picture of the original population.

Some comparisons between the mean lengths of age groups obtained from actual measurements and by back-calculation from similar samples taken in later years are shown in Tables 5, 6 and 7. Table 5 is compiled from fish caught in traps during the autumn (when growth for the year has been completed). The traps at this time of the year probably take fairly random samples of the population within certain size limits. It will be seen that in one of the four comparisons there is a difference of only 0·6 mm.

Table 5. *Female fish caught in pilot traps. Numbers in samples, mean lengths and standard deviations, of four pairs of samples. The first in each case is obtained from measurements of actual fish; the second by back-calculations from the same year class in a later year. The age group and the year caught of the sample measured or used for back-calculation are given in each case, as well as the value of* P *in a* t *test applied to the difference between the means of each pair*

Age group ...	I	II	II	III	II	IV	III	IV
Year ...	1942	1943	1942	1943	1942	1944	1943	1944
Mean length (cm.)	10·89	11·23	14·24	14·13	14·24	13·87	15·87	15·81
Number	25	23	50	51	50	11	51	11
S.D.	0·554	0·888	0·977	0·849	0·977	0·886	0·905	0·557
P	$0{\cdot}11 < P < 0{\cdot}12$		$0{\cdot}54 < P < 0{\cdot}55$		$0{\cdot}21 < P < 0{\cdot}22$		$0{\cdot}77 < P < 0{\cdot}78$	

Table 6. *Similar comparisons to those in Table* 5 *for two age groups of female fish angled in* 1944 *and* 1945

Age group ...	IV	V	V	VI
Year ...	1944	1945	1944	1945
Mean length (cm.)	17·92	17·90	17·94	17·87
Number	71	68	26	11
S.D.	0·950	0·782	1·119	0·964
P	$0{\cdot}89 < P < 0{\cdot}90$		$0{\cdot}84 < P < 0{\cdot}85$	

Table 7. *Numbers in samples, mean lengths, and standard deviations of O group fish in the spring of* 1940, 1941, 1942 *and* 1943 *obtained from measurements of netted samples, and by back-calculations from three samples of older fish netted in* 1944

Year	Statistic	Actual measurements from netted samples	Back-calculated from operculars		
			26 July 1944	25 Aug. 1944	28 Sept. 1944
1940	Number	201	4	3	0
	Mean length (cm.)	5·07*	6·19*	6·05	—
	S.D.	0·65	0·49	1·26	—
1941	Number	129	25	20	10
	Mean length (cm.)	6·19	5·96	6·21	6·17
	S.D.	0·81	0·75	0·91	0·91
1942	Number	467	25	9	15
	Mean length (cm.)	5·43	5·45	5·67	5·53
	S.D.	0·60	0·59	0·71	0·92
1943	Number	192	62	31	11
	Mean length (cm.)	5·46†	5·39	5·18†	5·57†
	S.D.	0·60	0·43	0·70	0·45

* For the difference between these means by *t* test $P < 10^{-5}$.

† For the difference between these means by *t* test $0{\cdot}03 < P < 0{\cdot}04$.

and that although in the other three there are differences of 3·7, 3·4 and 1·1 mm., in all cases the values of P derived from applying the t test (Simpson & Roe, 1939) show that these differences might well have arisen by chance. Table 6 shows two more comparisons for older fish taken from two comparable samples caught by angling, which is probably not selective within the size range of fish of these age groups. In both these cases the difference is very small, and very likely due to chance.

Both the above sets of comparisons deal with back-calculations made from fish 1 or 2 years older. In Table 7, however, are given some comparisons between means from measured samples of O group fish and means of back-calculations to the first winter ring from samples of fish from 1·5 to 4·5 years older. Both the successive annual samples of O group fish and the samples of older fish taken in 1944 were netted with seines of suitable mesh and so are likely to be good unselected samples. The mean of the 1943 fish back-calculated from the sample of August 1944 is significantly different both from the mean back-calculated from the September 1944 sample and the mean of the sample measured in 1943; the mean for the measured sample, however, lies between the two back-calculations. In all the other cases the difference is not more than 3 mm. In one of these cases, there is, however, a significant statistical difference between the back-calculated means derived from two of the samples; but the mean for the measured fish in this case lies between the two back-calculations.

This table suggests that there is a tendency, which is even more apparent from some other samples, for the lengths of fish back-calculated to the end of the first year to be slightly larger than the mean lengths derived from netted samples of fish a year old. This difference is not due to the correction for allometry, however, as when uncorrected these back-calculated lengths, especially from large fish, are generally smaller than the average lengths found by actual measurements. Measurements of the actual width on the opercular of this first ring suggest that there is a slight tendency for the ring to be wider in older fish than in fish 1 year old. It may be due, therefore, either to growth of the opercular inside the first annual ring after it is laid down, or to a differential mortality among fish of different sizes in their second year of life. The first possibility, of the growth of bone after it has been laid down, seems unlikely; but the second, a differential mortality, is probable. It is known that there is a heavy mortality among the young perch, and the length-frequency curves of fish of one age group very often show a positive skew, which may well be due to a mortality that is heavier among fish smaller than the mean, than among those larger. This difference between 'actual' and back-calculated lengths seems to occur only in 1-year old fish and is rarely large enough or frequent enough to be very important. Its exact significance cannot be determined from the data at present available.

The examples given above are supported by some additional comparisons that have been made, though not shown here. Where, however, there has been selection by the method of fishing employed to obtain the samples, there is often significant disagreement between back-calculated means and the means of corresponding measured samples. In such cases, however, there is usually comparable disagreement between the means obtained from separate samples, and between such samples and those obtained by unselective fishing methods. An example of such results obtained from comparisons between the mean lengths of different samples caught by slightly selective methods is given in Tables 8 and 9.

These data provide two sets of comparisons: (*a*) between the means of actual measurements made in 1943, and means back-calculated from measurements and operculars off fish caught in the same ways in 1944; and (*b*) between the means obtained from samples caught in two different series of traps: 'pilot' traps set at various depths through the spring, and in the fishery traps set through the spawning season from April to June.

The means have been compared statistically, and the differences, with their standard errors and the values of P giving the probability that as great a difference will arise by chance, are given in Table 9. There is significant disagreement between results from actual measurements and back-calculations in four cases, but in three cases the results from the two different series of traps, in the same year, are also in significant disagreement. In all other cases the differences are not significant. These comparisons show, therefore, that while in this case there are differences between the means from 1 year's samples and those back-calculated from the next year's samples, these differences are of the same magnitude as those between results obtained in the same year from two different samples. Both sets of differences are probably due to sampling errors, and possibly selective mortality in the intervening year. On the whole, then, it would seem as if the back-calculations of length agree with the lengths obtained by measurement of the same population of fish 1, 2 or 3 years before. It has been noticed that the means obtained by back-calculation before they were corrected for allometry, generally showed much greater differences among themselves and between the means derived from actual measurements than when corrected.

A few of the recoveries from a large number of fish that were marked in the late summers of 1943 and 1944 provide some additional evidence on the accuracy of the back-calculations. The majority of the recoveries were recaptured soon after they had been

marked and so had made no growth; none so far have been recovered which had completed more than one growing season. Fifteen fish provide information on back-calculated lengths and their details are given in Table 10. The initial measurements were made with live fish, and the lengths were recorded to 0·5 cm. in ments in particular, it is quite possible that the fish was recorded as belonging to the wrong 0·5 cm. or 1 mm. length group.

The marking took place near the end of the growing season and most of the fish that were recaptured during the subsequent winter showed no growth since

Table 8. *Numbers in samples, mean lengths and standard deviations, for four age groups of female fish in the spring of* 1943. *The two left-hand columns give the results from actual measurements made in* 1943, *the two right-hand columns the results of back-calculations made from operculars collected in comparable samples a year later*

		Actual measurements 1943		Back-calculated from 1944	
Age group	Statistic	Fishery traps	Pilot traps	Fishery traps	Pilot traps
I	Number	103	31	433	48
	Mean length (cm.)	11·66	10·81	10·85	11·09
	S.D.	0·81	0·60	0·87	0·98
II	Number	959	102	673	155
	Mean length (cm.)	14·09	14·33	13·88	13·96
	S.D.	0·74	0·90	0·79	0·78
III	Number	687	113	147	58
	Mean length (cm.)	15·04	15·41	14·99	15·30
	S.D.	0·86	1·12	0·96	1·05
IV	Number	63	15	12	3
	Mean length (cm.)	16·12	16·68	15·63	15·34
	S.D.	0·90	1·16	1·12	0·50

Table 9. *Comparisons between the means of Table* 8. *The two left-hand columns give the comparisons between the means calculated from actual measurements and back-calculations; the two right-hand columns give the comparisons between the two methods of trap fishing. The difference between the means, its standard error, and the value of* P *in a* t *test are given in each case*

		Comparisons between actual measurements and back-calculations		Comparisons between fishery traps and pilot traps	
Age group	Statistic	Fishery traps	Pilot traps	Actual, 1943	Back-calc. 1944
I	Difference	0·81	0·28	0·85	0·24
	S.E.	0·0903	0·1783	0·1345	0·1478
	P	$< 10^{-10}$	$0{\cdot}24 < P < 0{\cdot}25$	$< 10^{-9}$	$0{\cdot}10 < P < 0{\cdot}11$
II	Difference	0·21	0·37	0·24	0·08
	S.E.	0·0389	0·1087	0·0923	0·0693
	P	10^{-6}	$< 0{\cdot}001$	$0{\cdot}001 < P < 0{\cdot}01$	$0{\cdot}24 < P < 0{\cdot}25$
III	Difference	0·05	0·11	0·37	0·31
	S.E.	0·1066	0·1731	0·1270	0·1587
	P	$0{\cdot}63 < P < 0{\cdot}64$	$0{\cdot}52 < P < 0{\cdot}53$	$0{\cdot}001 < P < 0{\cdot}01$	$0{\cdot}05 < P < 0{\cdot}06$
IV	Difference	0·49	1·34	0·56	0·29
	S.E.	0·3421	0·4165	0·3208	0·4330
	P	$0{\cdot}16 < P < 0{\cdot}17$	$< 0{\cdot}01$	$0{\cdot}08 < P < 0{\cdot}09$	$0{\cdot}5 < P < 0{\cdot}6$

1943 and 1 mm. in 1944, so no great accuracy was obtained. Often, particularly in 1944, the length on recapture was not recorded very exactly either, sometimes due to delay in the return of the recaptured fish to the laboratory. Thus no very accurate comparison of actual and back-calculated lengths is possible. In Table 10 the range of length possible from the records made is shown; although, with the initial measure- being marked. Therefore the length recorded when the fish were marked should either lie between the back-calculated lengths for the winters preceding and following marking, or correspond to the length for the following winter. In Table 10 fish nos. 1–5 show a back-calculated length for the winter following marking which is in agreement (within the range of accuracy of the lengths) with the length on marking.

Fish nos. 6–12 show lengths on marking which lie between the lengths back-calculated for the preceding and following winters. In reading the opercular of these marked fish particular attention was paid to any false rings which might have been due to the check on growth by marking. In fish nos. 6–9 such false rings were observed, and the back-calculated lengths of the fish when they were laid down do correspond with the lengths on marking. In the case of fish no. 9, however, it is more likely that no growth followed marking that season and the length at the winter ring at the end of the season is the one that corresponds to the length on marking. In fish nos. 13, 14 and 15 the length at marking is slightly more than the length back-calculated for the following winter. The difference is in each case 1 mm.

conclusions drawn in these sections, that the opercular provides a useful and valid method for age and growth studies. There are, however, some features which may with advantage be further discussed.

The present study has been confined to material from only one locality, Windermere, but there is little doubt that the opercular method could advantageously be applied to other localities. A few opercular from other waters in Britain have been examined and they show annual rings very similar to those from Windermere and appear to be as easy to read. The opercular of perch from Sweden and Germany may also be judged from the accounts of Nilsson (1921) and Roper (1936) to be similar to those from Britain. It is unlikely that the appearance, or true annual nature, of the rings would vary with

Table 10. *Data from 15 recovered marked fish for comparison between recorded growth since marking, and back-calculations of growth from the opercular*

			Back-calculated lengths (cm.) at				
No.	Date when marked	Length (cm.) when marked	Winter ring before marking	Winter ring after marking	False ring in summer when marked	Final length (cm.) when recaptured	Date when recaptured
1	30 Aug. 1944	16·0	14·2	16·0	—	16·2	8 Aug. 1945
2	2 Sept. 1943	16·0–16·5	13·5–14·0	15·7–16·2	—	16·5–17·0	16 Aug. 1944
3	6 Sept. 1943	16·0–16·5	14·1–14·5	16·1–16·5	—	17·5–18·0	25 Aug. 1944
4	6 Sept. 1943	16·0–16·5	12·9–13·2	15·6–16·1	—	16·5–17·0	25 Aug. 1944
5	3 Sept. 1943	14·5–15·0	10·5–10·8	14·1–14·5	—	15·5–16·0	16 Aug. 1944
6	14 Sept. 1943	14·5–15·0	11·8–12·1	15·5–16·0	14·7–15·2	15·5–16·0	30 May 1944
7	13 Sept. 1943	16·0–16·5	14·5–15·0	16·5–17·0	16·1–16·6	16·5–17·0	13 Apr. 1944
8	14 Sept. 1943	17·0–17·5	14·6–15·1	17·5–18·0	16·9–17·4	17·5–18·0	8 May 1944
9	13 Sept. 1943	16·5–17·0	13·9–14·2	16·5–16·9	16·3–16·6	17·5–18·0	3 Nov. 1944
10	30 Aug. 1944	18·4	15·5	18·7	—	18·7	1 May 1945
11	30 Aug. 1944	16·2	14·5	16·8	—	16·8	6 Apr. 1945
12	13 Aug. 1943	18·5–19·0	15·8–16·2	19·5–20·0	—	19·5–20·0	30 May 1944
13	2 Sept. 1943	14·5–15·0	10·7	14·4	—	15·8	1 Sept. 1944
14	30 Aug. 1944	17·6	15·0	17·5	—	18·6	8 Aug. 1945
15	30 Aug. 1944	13·7	9·9	13·6	—	15·6	10 Sept. 1945

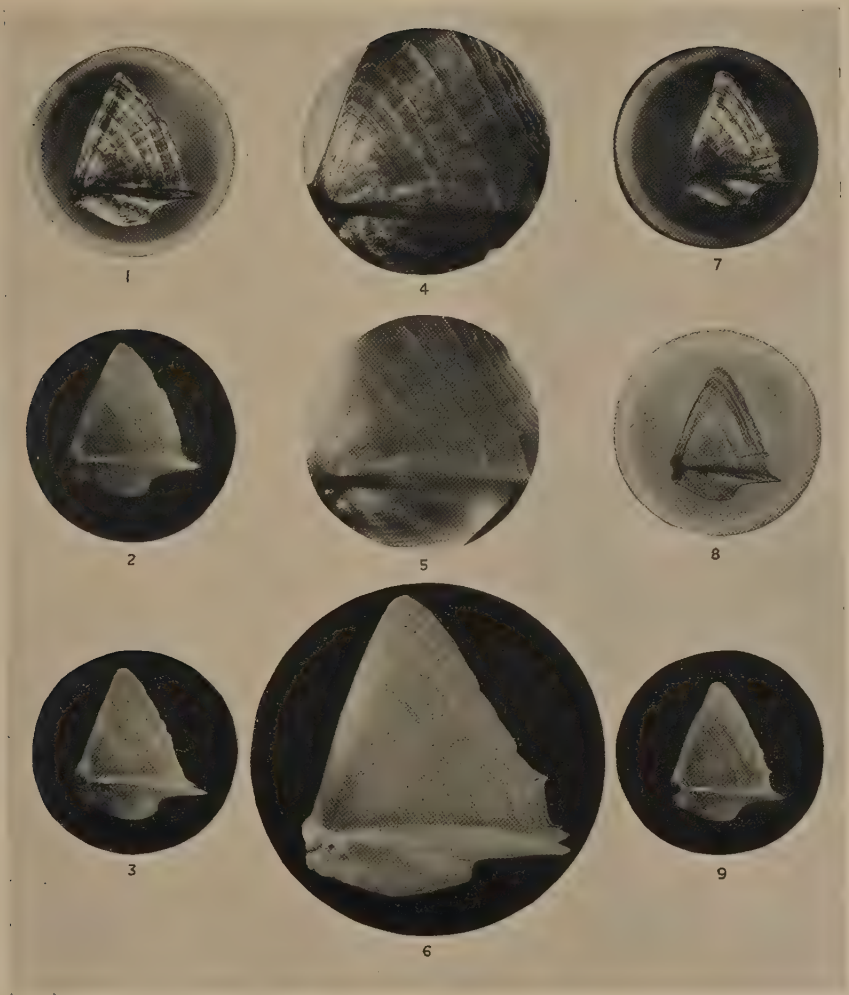
and although it may be due to inaccuracies in the method of back-calculation, it is just as likely to be due to an error in initial measurement. It is noticeable that in nearly all the examples in Table 10 if the back-calculated lengths had not been corrected for allometry the agreement between them and the actual measurements would have been very much poorer.

In 12 cases out of 15 therefore, there was agreement between actual measurements and back-calculated lengths within the rather inaccurate limits possible. In 3 cases there was disagreement but this was only slight.

7. DISCUSSION AND CONCLUSIONS

The previous sections have dealt with various aspects of the use of the opercular for age and growth determinations, and it is considered reasonable to conclude from the evidence presented and discussed, and the locality although it is possible that at the limits of its range, or where growth is exceptionally slow, or where the seasonal fluctuations in growth are abnormal, the rings might be difficult to interpret with accuracy.

Although there is thus little justification for doubting that the opercular can be validly used for determining the age of the perch in the majority of habitats, the widespread use of the opercular for back-calculating growth may not be so well founded if it is based on a formula for allometric growth derived from fish of only one locality. Isolated populations of fish often vary slightly in their shape and relative proportions and variations in proportions are very often the basis for separating some species into geographical races or species. It is therefore quite possible that growth rates for the lengths of opercular and fish do vary from one locality to another, and thus



1. Opercular from a 21·1 cm. fish, polarized light; by comparison with 2, this lighting exaggerates the mid-summer false rings; 5 winter rings (last on edge). 2. Same, reflected light; the true rings are clearer with this light, and false rings are not exaggerated. 3. Opercular from a 18·5 cm. fish, reflected light; a slow growing fish; innermost rings not clear, and there may be some false rings such as that between winter rings 3 and 4; probably about 9 years old. 4. Opercular from a 39·7 cm. perch, polarized transmitted light; 12 winter rings (one on edge); innermost rings not clear. 5. Same, transmitted light; innermost rings not very clear. 6. Same by reflected light on black background; 12 rings clearly seen; the abrupt change from dark to white (transparent to opaque) is clearly seen on most rings; there is a faint false ring in the 4th summer zone. 7. Opercular from a 17·0 cm. slow growing fish, polarised light; very complex outer rings; innermost rings clearer than in 8. 8. Same, transmitted light. 9. Same, reflected light; this gives the clearest picture of the rings, but it is difficult to be certain of the true winter rings; probably 8 years old; this is one of the most difficult operculars so far collected.

ideally the growth ratio should be estimated for each locality before back-calculations of growth are made from opercular from that locality. It is unlikely, however, that there is any very great variation, and it is probably safe to assume that approximately accurate results can be obtained from any locality using the growth ratio obtained for Windermere.

The discovery of a definite allometry in the growth of the opercular is of some interest in connexion with the widespread use of morphometric measurements in fish taxonomy. Subspecies or even species are separated largely on the basis of morphometric ratios often measured on one or a very few specimens, and so if allometry is common in the relative growth of different parts of fish, in some cases it may seriously affect the taxonomic criteria that are used.

It is realized that in attempting to show the accuracy of the readings of age and growth from the operculars the evidence presented is mostly of an indirect kind, and that there has been no direct check applied to the results. Direct checks that are applicable involve the recorded observation of fish kept in tanks or marked in large numbers in the field, which are laborious and of necessity long-term procedures. A study should also perhaps be made of the agreement between scales and operculars in the readings of age and growth obtained from them, employing Segerstrale's correction for scales and allowing for allometric growth in operculars. It is considered, however, that within the limits of accuracy usually required in research on fish ecology the data given in this paper do provide an adequate check on the use of the opercular bone, and that it is therefore legitimate to use the method for age and growth studies on the perch.

Although in certain species of fish the value of the opercular bone for age and growth determinations has been demonstrated, in work on most species, the scales and less frequently the otoliths are used. The otoliths suffer from the disadvantages that they are often difficult to extract and that they do not lend themselves to growth calculations. The use of the scales has one unique advantage in that it is generally possible to remove a few scales from a fish and then return it to the water alive. The opercular bone, however, has several useful characteristics. It is readily removed from the fish; it is easily prepared and is used dry, without any need for it to be mounted; and it is a useful size to handle and store. In the case of fish of the usual sizes encountered the opercular is large enough for the annual rings to be seen with the naked eye, yet with adequate optical apparatus an image can be projected for detailed examination and growth measurements. It would seem then as if the opercular bone possessed several useful, practical advantages, and that when studying species where the scales are found to be difficult, investigation of the possibility of using the opercular might prove fruitful.

8. SUMMARY

1. The use of the opercular bone in determining the age and growth of the perch in Windermere is described.

2. The readings of age from the operculars of fish up to 4 years old at least, agree with estimates of age made from length-frequency distributions, and are also confirmed by the occurrence of dominant year classes in successive annual samples.

3. The opercular shows allometric growth in relation to the length of the fish. The correction of directly proportionate back-calculations of growth is described.

4. There is little direct evidence to check the accuracy of the back-calculations of growth, but the evidence available in general shows that these calculations are reasonably accurate.

5. It is concluded that the use of the opercular provides a good general method for ascertaining the age and growth of the perch.

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RELATIONS BETWEEN NUMBER IN BROOD, FEEDING-RATE AND NESTLING PERIOD IN NINE SPECIES OF BIRDS IN TANGANYIKA TERRITORY

By R. E. MOREAU

Especially in view of the recent work on the significance of clutch-size (Lack, 1947), it is desirable to ascertain to what extent parent birds adjust the frequency of their feeding visits to the number of young in the nest; whether in the amount of food they receive the members of larger broods are at any disadvantage compared with those of smaller broods; and whether a lower feeding-rate is correlated with slower development of the young in the nest.

This study is based primarily on about 5000 hr. of observations made by supervised African observers between 1937 and 1946. They are selected from the later stages of the nestling periods, when the feeding activities of the parents were not confused by brooding. All the work was done at Amani, in Tanganyika Territory at 5° S., except for one species, the *Colletoptera*, which was studied about 50 miles away on the shores of the Indian Ocean. Amani is an evergreen locality in which forest of an especially luxuriant type predominates, as described elsewhere (Moreau, 1935); but most of the data on which the present analysis is based are derived from hirundines and swifts nesting in clearings.

The length of day in these latitudes is always within 20 min. of 12 hr., and the active period of all diurnal birds, including swifts, varies throughout the year only between about 12½ and 13 hr. The observations were made in continuous spells of 7 or 8 hr. as a rule, but occasionally from dawn to dusk; and for each nest from 4 to 13 days of observations are available for the present purpose. As I have had occasion to remark before, I am satisfied of the general reliability of the Africans' work.

In the detailed accounts I have already published of the breeding biology of some of the birds here dealt with, feeding-rates were calculated on a time-unit of 200 min., since the hour is an inconveniently short unit for recording activity of swifts. However, the use of the 200-min. unit has given rise to some difficulty and misconception. In the present study all feeding-rates have therefore been calculated per hour, although for the swifts the result is a series of fractions. In other species, where the feeding rates are big enough, I have worked to the nearest whole number.

The possibility cannot in most species be excluded that on particular days or in particular nests lower feeding-rate may be correlated with, and so off-set by, bigger or more numerous morsels per visit. However, in each species such cases presumably occur irrespective of number in brood, so that they would not invalidate a comparison between the means, or the ranges, of feeding-rates for the respective numbers-in-brood.

Nestling periods (hitherto called 'fledging periods') are calculated by the methods advocated elsewhere (Moreau, 1946; Moreau & Moreau, 1940). As there emphasized, one is justified in quoting a nestling period without indicating a margin of error only when the time and date of hatching and the time and date of flying are known for the individual nestling. These conditions are hardly ever fulfilled in field observations, especially when the brood consists of two or more young that have not been distinguished from birth. The margin of error and 'spread' arising from these causes must be admitted; and can conveniently be given numerical expression by calculating the longest and the shortest periods that can be derived from the data, and quoting the nestling period as the mean of them ± half the difference between them.

Where the eggs in a clutch of two hatch close together, but the young leave the nest well apart—up to 96 hr. is not rare in palm-swifts—it is useful to calculate more than one nestling period for the brood, one based on the earlier flying date and the other on the later, each with a margin of error that includes the 'spread' in the hatching. The same method can of course be applied when a difference between hatching dates is established; and moreover it can be extended to broods of more than two.

In the swallows and rock-martins there is danger in nests not under continuous observation that first flyings will go undetected, because individual young, after being out of the nest for a few minutes or hours, are apt to return to it, not merely to roost. In the other species dealt with this source of error is excluded, since the young, once they have left the nest, apparently never return to it.

Table 1 presents a general summary of the results and relevant details for each of the nine species, notes on each of which follow. The feeding-rates in Table 1 have been obtained by (1) calculating for each nest the average feeding-rate for each day's observations, (2) obtaining from these daily averages an average for

each nest. The figures inserted in col. 3 are the lowest and the highest nest averages obtained for the number-in-brood indicated; and those in col. 4 are the averages for all the nests having that number-in-brood. The data are not sufficient for the averages for the numbers-in-brood in each species to be compared statistically.

In col. 5 of Table 1 those fledging periods given in italics are means and standard deviations based on a larger number of nests than those for which the feeding-rates are recorded. In other cases the figures given are the shortest and the longest nestling periods recorded for the nests referred to in col. 2. The nestling periods given in brackets are isolated records of virtually no value for the present purpose.

Table 1. *Summary of feeding-rates*

Species and number of hours of observations (1)	Broods for which data are available (2)	Feeding-rate per nestling per hour: Individual nest averages (3)	Feeding-rate per nestling per hour: Overall average (4)	Nestling period with standard deviation (S.D.) (days) or range* (5)
Rock-martin 1300	3 × B/1	11–13	12	(21 ± 1)
	14 × B/2	3·5–13·5	9	*22·5*† S.D. *2·33*
	11 × B/3	5·3–12 (21)	8·8 (10)	*24·05*† S.D. *3·26*
Stripe-breasted swallow 450	2 × B/2	3·5–9	6·2	18½ ± 1½–21½ ± 1½
	6 × B/3	2·6–7·3	5	17½ ± ½–21½ ± ½
Wire-tailed swallow 600	1 × B/1	16	[16]	(18½ ± ½)
	3 × B/2	12·5–14	13·2	19 ± 1–20½ ± ½
	7 × B/3	5–11·3	8·5	18 ± ½–21 ± 1
Bank-martin 500	3 × B/1	2·4–4	3·1	24 ± 1–25½ ± 1
,,	7 × B/2	1·9–2·4	2·2	23½ ± ½–27½ ± ½
Palm-swift 1000	9 × B/1	0·9–1·3 (1·75)	1·1 (1·2)	*35·0* S.D. *2·9*
	12 × B/2	0·6–1·15	0·93	*35·8* S.D. *4·05*
White-rumped swift 800	5 × B/1	0·3–0·55 (0·8)	0·46 (0·53)	*42·2* S.D. *3·27*
	8 × B/2	0·35–0·55	0·47	*41·7* S.D. *3·8*
Little swift 300	2 × B/1	0·5–0·55	0·52	38 ± 1–39 ± 1
	2 × B/2	0·35–0·4	0·37	(38 ± 2)
	2 × B/3	0·32–0·35	0·33	—
Paradise flycatcher 300	1 × B/2	4·2	[4·2]	(10½ ± ½)
	2 × B/3	1·7–2·0	1·85	11½ ± ½–11¾ ± ¼
Mountain wagtail 100	1 × B/1	4·4	[4·4]	(16½ ± ½)
	1 × B/2	2·9	[2·9]	(15⅝ ± ⅜)

* Italics show figures based on additional numbers of broods as given in the text. Ranges are calculated as explained in para. 2, p. 206.

† Statistically significant difference.

Red-throated rock-martin (*Ptyonoprogne fuligula rufigula* (Fschr. & Rchw.))

A nest-behaviour study of this species is in preparation. The nest is a shallow cup attached by one edge to a vertical surface and always under overhead cover, in this case under the eaves of buildings of European type. The feeding of the young can be well observed. Food is transferred instantaneously from the parent, which in the later stages of the nestling period hardly alights and hardly ever tenders food to more than one of the young in the nest at any one visit. At any rate at Amani, each pair has a small and sharply defined territory in which all the food from the family is obtained. The young are liable to return repeatedly to the nest after first leaving it.

At some of the nests, the parental attention was highly consistent, but at most nests the highest mean feeding-rate for an individual day was at least one and a half times the lowest. At some nests, the day-to-day fluctuations were wild, e.g. 6–18 and 4–12·5, and they were not connected with weather. On the other hand, at the two nests that give the high and the low extremes for the species, 13·5 and 3·5 feeds per individual per hour, parental attention was consistently good and bad respectively.

The feeding-rate of 21, bracketed in Table 1, provides a striking case of over-adjustment by the parents. When their brood of one two-thirds-grown young was increased to three they quintupled the rate of their visits to the nest; and the result was that the feeding-rate per young bird became one and a half times as great as the next highest of which there is any record. Moreover, the abnormal rate of a visit a

minute to the nest was maintained for the 6 days till the young flew. In Table 1 the overall average of 10 includes the 'unnatural' nest average of 21 and the overall average of 8·8 excludes it.

It seems clear from Table 1 that on the average a member of a trio in a nest got practically as much food as a member of a pair. For 22 of the nests the nestling periods are known, and when these are tabulated against the average feeding-rates at the nests concerned inspection suggests no correlation. But an interesting result is obtained by using the whole of the nestling periods available for this species, which total 4 for solitary young, 68 for members of pairs and 96 for members of trios. Discarding the data for the solitary birds as being too scanty, the mean nestling period for members of pairs is 22·5 days, S.D. 2·33; and for members of trios 24·05 days, S.D. 3·26. The difference is statistically significant. For this result no reason can be suggested.

Lesser stripe-breasted swallow (*Hirundo abyssinica unitatis* (Scl. & Praed))

This swallow builds a closed 'retort' nest in the angle between a vertical face and overhead cover. The Amani nests were all between wall and ceiling, at the top of a window-recess or under a horizontal wooden sun-screen. Since actual feeding cannot be observed visiting-rate has had to be accepted as feeding-rate. Moreover, there is difficulty in counting the young before they emerge. These possible sources of error might seem partly accountable for the amazing differences in feeding-rate recorded for this swallow: but such differences are paralleled in those for *Ptyonoprogne* and other species using nests perfectly open to observation.

In the stripe-breasted swallow the feeding-rate, calculated on long series of hours at each nest, can vary between nests up to nearly three times the minimum, namely in broods of two from 3·5 to 9, and of three from 2·6 to 7·3. The highest individual feeding-rate for the species is in a nest containing a pair of young; but so is the lowest feeding-rate but one. By comparison the feeding-rates at each nest are consistent, varying from day to day by not more than half the lowest.

The data available for nestling periods (at seven nests) do not suffice for statistical treatment, but suggest on inspection no correlation between feeding-rate and nestling period.

Wire-tailed swallow (*Hirundo s. smithii* (Leach))

A preliminary account of behaviour at three of the nests has already appeared (Moreau, 1939*a*). The nest of the species is an open cup stuck to its (vertical) support by one edge, and under cover; those at Amani were on walls and close to the top.

Table 1 shows that a member of a trio in a nest is very likely to get more food than a member of a pair; but when the nestling periods for these nests are tabulated alongside the feeding-rates no correlation between them is suggested. In fact the shortest nestling periods recorded for the species are for broods with individual feeding-rates of 7·7 and 16.

As a rule in this species the male and female (which are distinguishable) share the work fairly equally. It is therefore noteworthy that when the male died at one nest containing three young his mate unaided maintained consistently the feeding-rate at slightly above the average.

Rough-wing bank-martin (*Psalidoprocne h. holomelaena* (Sundev.))

An account of behaviour based on most of the nests here dealt with has been published (Moreau, 1940). As the nest is in a tunnel, usually in a shady bank, the actual feeding cannot be seen and visiting-rate has to be taken as feeding-rate. The species is, however, uncommonly regular in feeding-rate both at the individual nest and as between nests.

The evidence seems conclusive that the individual nestling gets more food than a member of a pair (Table 1). The data exclude the possibility that a lower feeding-rate results in a longer fledging period.

Palm-swift (*Cypsiurus parvus myochrous* (Rchw.))

The breeding biology has been described elsewhere (Moreau, 1941). The nest, made of feathers and saliva, is stuck on the more or less vertical surface of a hanging palm-frond. Since it is practically no more than a vertical pad providing no cavity, the eggs are glued to it with saliva and the young birds, which are hatched with strong claws, have to cling to it throughout their nestling period. The nests at Amani were exceptional in being so close to the ground that, in those selected for observation, every operation could be clearly seen.

Attention to both eggs and young is extremely irregular at every stage. Feeding continues throughout daylight, but is accelerated in the hour before the birds go to roost to such an extent that feeding-rates calculated on an observation period that includes this hour are not comparable with rates based on periods that do not. Therefore for the present purpose this hour is excluded in all cases. The average feeding-rate for the entire 13-hr. day is always higher than the figures here given. At a nest containing two young as many as six feeds may be brought in the last hour.

Table 1 shows that on the average solitary young birds receive more food than members of pairs. Two nests in which one of the pair of young disappeared in the course of the observation period are instructive in this connexion: in one the feeding-rate per individual

young rose, after the second nestling had gone, from 1·0 to 1·3 and in the other from 0·6 to 1·0.

The variation in length of nestling period is noteworthy, the longest being actually half as long again as the shortest; yet there is no clear relation between feeding-rate and nestling period. Two young of a pair often fly 4 days apart. Exceptionally long nestling periods of 43 days (twice), 44 and 48 (twice) are well authenticated and I have no reason to suspect them.

Nestling periods are available for altogether 9 solitary young and 64 members of pairs. The mean nestling period for the former is 35·0 days, S.D. 2·9; for the latter 35·8 days, S.D. 4·05. The difference is not significant.

White-rumped swift (*Micropus caffer streubelii* Hartl.)

An account of the breeding of this species has appeared (Moreau, 1942*a*). The swifts always use other birds' nests, usually the closed 'retorts' of stripe-breasted swallows, in which case feeding has to be inferred from entry of parent.

Parental attention is at all stages remarkably erratic. There is no feeding rhythm in the course of the day, and no special 'stoking' in the last hour of daylight as in the palm-swift. Since the young swifts, once out of the nest, do not return, the nestling periods are regarded as reliable, however excessive some may appear.

The highest feeding-rate recorded in Table 1, 0·8, is to a solitary nestling, but in arriving at an average rate for solitary young this record should perhaps be ignored. The nest contained two young until one disappeared at 22 days old, the day before the observations on which the average of 0·8 is based. Records are, however, available also for the 14th–22nd days of the two young, when the average combined feeding-rate was 0·7, only 0·35 each. If we omit this abnormal figure of 0·8, there is no practical difference between the feeding-rates of solitary white-rumped swift nestlings and members of pairs of nestlings.

Nestling periods are available altogether for 19 young that were solitary for all or most of their time, and for 160 young that were members of pairs throughout. In the former the mean nestling period was 42·2 days, S.D. 3·27; in the latter 41·7 days, S.D. 3·8 (not significantly different).

Little swift (*Colletoptera affinis abyssinicus* (Streubel))

The nestling biology has been described (Moreau, 1942*b*), but unfortunately few nestling periods were obtained because the observer was ill about the time most of the young were leaving the nest. The nest is a closed one under eaves or a rock-shelter, so that the feeding of the young cannot be actually observed. Feeding takes place throughout the hours of daylight, and there is no change in rate with time of day.

Table 1 shows clearly that the more young in the nest the lower the individual feeding-rate, but data on nestling periods are insufficient to show whether they were in any way related to feeding-rates.

Paradise flycatcher (*Tchitrea perspicillata ungujaensis* G. & M.-P.)

An account of behaviour based on 300 hr. at three nests has been prepared. Male and female share the nest duties about equally. The nest is a beautiful neat cup built of moss and lichen on a twig over water, so placed that all occurrences can be well observed.

It is most remarkable that a brood of two consistently received more feeding visits than either of two broods of three, and that the individual young birds of the pair received more than twice as many visits with food. This applied not only to the later days of the nestling period, with which this paper is concerned, but also to the earlier, before the young ceased to be brooded. There is evidence, moreover, that the individual feeds to each young of the pair were at least as big as to each of the other young. The best-fed brood certainly flew after a slightly shorter nestling period than the worst-fed and probably than the medium-fed. But whereas the best-fed apparently received nearly two and a half times as much food as the worst-fed, the nestling period of the latter was at most one and a fifth times that of the former.

Mountain wagtail (*Motacilla clara torrentium* Ticehurst)

Data are available for only two nests where, however, the consistency of feeding-rate was noteworthy. That of the brood of two (5·3–6·0) was always higher than that of the solitary nestling (3·6–5·1), but always lower per individual. The nestling period was almost certainly longer for the best-fed bird.

SUMMARY

1. Feeding-rates for four species of hirundine, three of swift, one of paradise flycatcher and one of wagtail, derived from about 5000 hr. of observations at 102 nests in Tanganyika Territory, are summarized. Additional nestling periods are available, making in all about 500 for these species.

2. In most of the species for which there is a good volume of data, feeding-rate per nestling varies greatly both from day to day in some of the nests and as between nests (calculated on the mean of all the data available for each). In several species ranges in feeding-rate per nestling for different numbers-in-brood overlap widely. As a rule, the more young in the nest the more frequent the parents' visits, but not in proportion to the increase in the number of young; so that on the average a solitary nestling gets more food than a member of a pair or of a trio. Two species for which there is, as it happens, the biggest volume of

data, are however to some extent exceptions: there is practically no difference (*a*) in the white-rumped swift (*Micropus caffer struebelii*) between the feeding-rate of a solitary young bird and that of a member of a pair, (*b*) in the red-throated rock-martin (*Ptyonoprogne fuligula rufigula*) between members of a pair and members of a trio.

3. There is no evidence that higher feeding-rate is correlated with shorter nestling period in any species but the paradise flycatcher (*Tchitrea perspicillata ungujaensis*), where there is only an isolated observation.

4. On correlation between feeding-rate and nestling period of individual young the data do not suffice for statistical examination, but inspection of detailed records (not here reproduced) gives no satisfactory indication that lower feeding-rate is correlated with longer nestling period.

In three species nestling periods are recorded for many nests in addition to those for which feeding-rates are available. They show no statistically significant difference between the nestling periods of solitaries and pairs in the white-rumped swift (where there is no difference in the feeding-rates) and none in the palm-swift (*Cypsiurus parvus myochrous*) (where there is a difference in the feeding-rates). But in the rock-martin the nestling period averages 1·5 days longer (a significant difference) in trios than in pairs, though there seems to be no difference in the feeding-rates.

5. Apart from this last anomalous result, the general conclusion drawn from this study is that the greater the number in brood the less food each is likely to receive and, since nestling period is not prolonged in proportion to drop in feeding-rate, the less the individual is likely to weigh when it leaves the nest.

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ON THE ECOLOGY OF BEETLES OF THE GENUS *AGRIOTES* WITH SPECIAL REFERENCE TO *A. OBSCURUS*

E.H.N.

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(With 6 Figures in the Text)

1. INTRODUCTION

The habits in this country of the adult of the common wireworm have been studied in detail by Miles & Cohen (1939–40) and Cohen (1942). Gough & Evans (1942), besides pointing out certain distributional peculiarities, started experimental work on movement in the field and ovipositional preferences. The extensive studies of wireworm distribution by Salt & Hollick (1946) yielded correlations between population density and various environmental factors, and the value of investigations into the biological bases of these associations became apparent. In section 4 of this paper an experiment is described by which it was attempted to test the effect of that form of environmental selection which could be exercised by the influence of plant species on the fecundity and longevity of the adult *Agriotes*. Studies on distribution, activity and movement are also described.

2. DISTRIBUTION

Attention has been drawn by Gough & Evans to the very variable proportions of *Agriotes sputator* (L.) and *A. obscurus* (L.) caught in different fields on the same farm, and they have attributed this species 'patchiness' to low individual mobility. Salt & Hollick have shown a tendency for the segregation of '*obscurus-lineatus*' from *sputator* in a small grass plot near Cambridge. As it was necessary to collect beetles for an experiment on nutrition described later in this paper, opportunity was taken of investigating the distribution within a single field.

The field selected, area 8 acres ('Stackyard', Fig. 1*a*), had been pasture for 18 years and was ploughed on 19–20 March 1946. The soil is a heavy gravelly loam, on clay with flints. Twenty traps were set in six rows as in the figure. Each trap consisted of a bunch of cut grass and covered about 1 sq.ft. of soil which had been stamped down to form a firm substratum. Every day, fresh grass was added, and a corresponding quantity (about a fifth of the total trap) of old grass was removed. In this way a mixture of grass 1–5 days old was maintained in each trap, and variability due to the effect of the age of grass on its attractiveness was reduced. The beetles were removed in the early morning by shaking them into a white cloth.

The mechanism of such traps has nowhere been analysed, but it is probable that the beetles are induced to enter in a search for shelter and food. As such, the efficiency is very much dependent upon environment, being influenced by climate, the species and amount of the surrounding vegetation, and the extent to which the soil surface itself offers shelter. In addition to this, it is not known to what extent variables such as the species, sex and mobility of beetles affect their liability to capture. In spite of these disadvantages, however, such traps can quite reasonably be used for comparing the *Agriotes* fauna, from areas having sufficiently the same immediate climatic and vegetational sequence and topography as can be found within many cultivated fields in this country. As long as all traps are subject to the same environmental fluctuation and trend they remain comparable, and in such circumstances may even be used to seek such trap-time interactions as would be exhibited by seasonal migration of the beetle population.

The first captures were made on 20 March 1946 soon after the spring rise in temperature trend, but emergence was gradual and evidence will later be presented which indicates that it was not complete until 9 or 10 April. The aggregate of 10 days' catch from the 20 traps during the period 29 March–4 May 1946 was 2271 beetles, composed of 1647 *A. sputator* (L.), 524 *A. obscurus* (L.), 98 *A. lineatus* (L.), and 2 *A. acuminatus* (Stephens). An analysis is presented in Table 1 (*A. acuminatus* omitted and *A. lineatus* not analysed owing to insufficiency).

Both *A. sputator* and *A. obscurus* showed variable density over the field, but these densities were not significantly correlated

$$(r = -0{\cdot}230 : 5\,\%\ \text{point} = 0{\cdot}444).$$

A simple contour map was plotted (Fig. 1*b*, *c*) and it became apparent that the distribution was probably not merely 'patchy', but showed several trends. Thus *obscurus* was relatively high round the north-east and north-west sides and reached a peak in the east corner whilst *sputator* occupied the centre but extended to the edge in places. These differences

were reflected in the sign of the correlation coefficient, and were clearly of the same type as those found in Sheep's Green by Salt & Hollick (1946), although the proportion of *obscurus* plus *lineatus* to the whole population never exceeded 62% (trap 3) and never fell below 5% (trap 14).*

During the same period and extending a little longer (29 March–11 May 1946) the east corner of the field was subjected to a more intensive examination. Ten traps (A–J in Fig. 1*a*) were set 15 yd. apart in the form of an equilateral triangle, trap G of this series being the same as trap 1 in the other series. The sums of 17 separate day-catches are shown in Table 2, together with an analysis of the transformed data.

In this part of the field, the number of *obscurus* caught nearly equalled the number of *sputator*, and there were also many *lineatus*. Analysis revealed no significant differences between trap-catches for the second species, but for *obscurus* and *lineatus* differences did exist. These, in the case of the former species, indicated that the smaller populations obtained in the three south-westerly traps (H, I and J) might have been genuine, a fact which fits in with the conjectured density distributions as depicted by contours in Fig. 1*b*, *c*. In the case of *lineatus* trap E showed a notably high yield and trap H a very low one. If the explanation of such differences, which were presumably generated under pasture conditions, but yet persisted through 5 weeks of bare to small

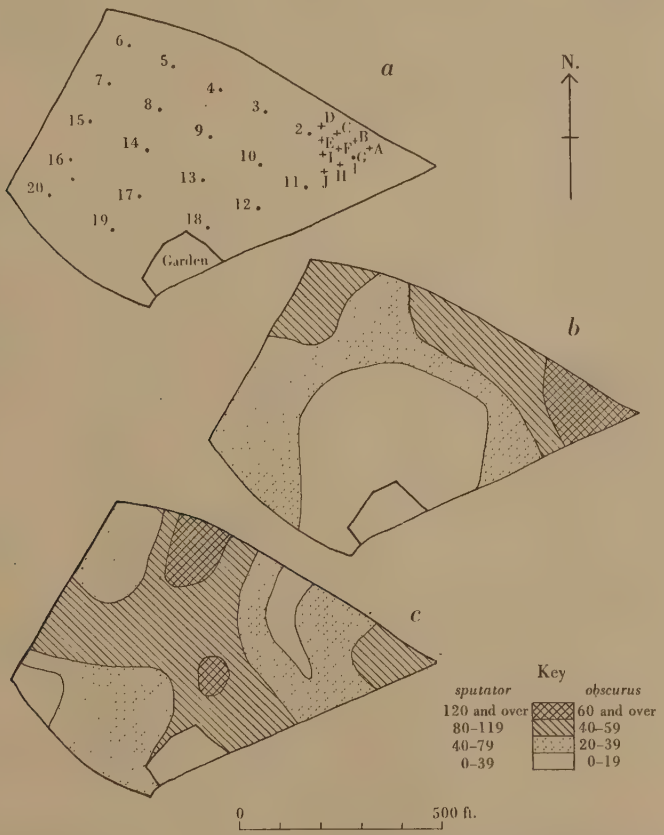

Fig. 1. Stackyard: plan of samples (*a*), and density distribution of *Agriotes obscurus* (*b*) and *A. sputator* (*c*).

* In Sheep's Green the corresponding figures were: for stations 11–13, 72·7, 71·4 and 62·9% respectively (maxima) and for stations 1–7 all values were below 5% (minima).

wheat vegetation, lay in the sedentary habits of the beetles, their effective movement must have been very small indeed.

In this connexion a rough calculation of the area from which beetles were drawn into a trap is illuminating. The wireworm population of the field had been estimated by samples using the separation technique developed by Salt & Hollick (*in lit.*); from this, the number of adults expected per sq.yd. may be calculated if it is assumed that they constitute 2 % of the population (figure given by Salt & Hollick, 1944, p. 62).* In Table 3 the calculation is made for the whole field and also for the east corner.

From these figures it appears that in order to supply the material caught, beetles need only have come from a distance of 1 yd. on the average.*

Further analysis of the trapping data by the method of covariance produced some interesting comparisons between the species. The relevant correlation and regression coefficients are set out in Table 4.

No significant correlation was shown between the spatial distributions. The coefficient between *obscurus* and *sputator*, although small, was not negative, but an interesting possibility of a closer positive relation between *obscurus* and *lineatus* was indicated.

Table 1. *Analysis of the* Agriotes *sp. caught in* 20 *traps for* 10 *days on Stackyard from* 29 *March to* 4 *May* 1946

Trap	Total of 10 days' catch			Sum of transformed† trap-day catches	
	A. sputator (*X*)	*A. obscurus* (*Y*)	*A. lineatus* (*Z*)	*A. sputator*	*A. obscurus*
1	84	66	14	8·228	8·161
2	58	51	18	5·674	6·871
3	29	40	8	5·103	6·212
4	91	40	1	8·508	5·738
5	165	31	1	10·376	4·760
6	62	41	3	7·691	5·837
7	64	45	6	6·392	5·592
8	101	20	0	8·166	3·413
9	107	9	2	8·407	2·883
10	51	7	0	6·598	1·806
11	41	25	11	5·631	4·258
12	89	17	13	7·250	3·179
13	133	12	2	9·947	2·350
14	111	6	0	9·428	1·681
15	81	26	1	8·064	3·846
16	106	26	7	9·011	3·664
17	55	5	1	5·893	1·204
18	103	9	0	8·538	1·954
19	78	14	5	8·194	3·079
20	38	34	5	5·216	4·450
Total	1647	524	98		

Standard error of differences between transformed sums for *A. obscurus* = ± 1·20, *A. sputator* = ± 1·11.

Analysis of variance of transformed data

Source of variation	Degrees of freedom	*A. sputator* (*X*)		*A. obscurus* (*Y*)	
		*Sx*²	Mean square	*Sy*²	Mean square
Total	199	37·631	—	25·911	—
Days	9	22·265	2·474‡	6·634	0·737‡
Traps	19	4·734	0·249‡	7·009	0·369‡
Error	171	10·632	0·062	12·268	0·072

† The data were subjected to a logarithmic transformation.
‡ Indicates that the mean square value is less than 1 % probable.

* This is the best figure available, but there are many reasons why it may not apply precisely to these conditions, e.g. the small size of the present sample, the possible difference in species content, etc.

* It will be noticed that a trap is expected ultimately to reduce the beetle population in its area; but such effects were not detected in this work owing to the high day-to-day variability in catch.

Table 2. *Analysis of the* Agriotes *sp. caught in* 10 *traps for* 17 *days on the east corner of Stackyard from* 29 *March to* 11 *May* 1946

Trap no.	Total of 17 days' catch			Sum of transformed* trap-day catches		
	A. sputator (*X*)	*A. obscurus* (*Y*)	*A. lineatus* (*Z*)	*X*	*Y*	*Z*
A	107	102	42	11·557	12·336	7·043
B	138	113	17	13·207	13·148	3·839
C	95	103	32	11·009	13·219	6·140
D	104	88	29	11·729	10·286	5·219
E	119	122	82	11·167	13·635	10·695
F	115	126	21	10·579	12·926	4·684
G	123	111	20	11·753	11·815	4·237
H	66	70	4	9·190	10·201	1·079
I	90	69	18	10·644	9·691	4·061
J	133	57	33	12·419	8·212	5·344
	1090	961	298			

Standard error of differences between transformed sums for *A. obscurus* = ± 1·52, *A. sputator* = ± 1·49, *A. lineatus* = ± 1·31.

Analysis of variance of transformed data

Source of variation	Degrees of freedom	*A. sputator* (*X*)		*A. obscurus* (*Y*)		*A. lineatus* (*Z*)	
		Sx^2	Mean square	Sy^2	Mean square	Sz^2	Mean square
Total	169	32·264	—	24·162	—	17·436	—
Days	16	22·285	1·393†	12·722	0·795†	6·880	0·430†
Traps	9	0·638	0·071	1·781	0·198†	3·283	0·365†
Error	144	9·341	0·065	9·659	0·067	7·273	0·051

* The data were subjected to a logarithmic transformation ($n+1$).
† Indicates that the mean square value is less than 1 % probable.

Table 3

	Whole field	East corner
No. of beetles expected per sq.yd.	3·1	8·9
Mean no. of beetles caught per trap per day	11·35	13·8
Therefore minimum area from which drawn (sq.yd.)	3·66	1·55
Radius of circle of this area (yd.)	1·08	0·70

Table 4. *Correlation and regression coefficients relating the transformed numbers of* Agriotes sputator (*X*), A. obscurus (*Y*), *and* A. lineatus (*Z*), *occurring in traps on Stackyard*

		Correlation coefficients			Regression coefficients	
		Traps	Days	Error	Days	
Whole field	*XY*	−0·230	0·808*	0·209*	0·44	(*Y* on *X*)
East corner	*XY*	0·078	0·755*	0·247*	0·57	(*Y* on *X*)
	XZ	0·260	0·848*	0·018	1·52	(*X* on *Z*)
	YZ	0·450	0·879*	0·372*	1·20	(*Y* on *Z*)

* Indicates that the mean square value is less than 1 % probable.

(5% point $r=0{\cdot}632$.) No tendency for segregation of *obscurus* and *lineatus* from *sputator* was discernible in this plot.

The marked day-to-day variance in total transformed catch (see Tables 1 and 2) was highly correlated between all three species, and indicated a qualitatively common reaction to certain climatic elements.

Emergence from the soil

(*a*) *In relation to species*

Reference has already been made to the prolonged period of emergence from the soil (20 March–9 or 10 April). Population proportions which were maintained in the east corner of the field after the 9 April (and up till 11 May when trapping ceased) were only arrived at gradually. From 2 to 8 April *sputator* 11 May, both of which were internally reasonably homogeneous. Similarly, *sputator* showed a decline from 1·10 to 0·60 between the same periods (5–13 April and 2–11 May). It is interesting to note that at corresponding stages in the season the ratio males/females was higher in *obscurus* than in *lineatus* which was in turn higher than in *sputator*, thus providing one more example of the differences between these three species.

3. ACTIVITY AND MOVEMENT

(*a*) *Activity*

(1) *General*

Adults of *Agriotes obscurus* have well-defined diurnal alternations of activity and quiescence which are modified by environmental fluctuations. During quiescence the beetles lie under stones or near the soil surface under tangled vegetation. Activity takes various forms: walking, flying, feeding, copulating and ovipositing. In order to gain some measure of the period and intensity of activity of *obscurus*, beetles were kept in an enclosure containing an automatic recorder.

Table 5. *Summary of sex ratio data*

Period	Actual			Percentage		Ratio:
	Males	Females	Total	Males	Females	males/females
			A. obscurus			
28 March–1 April	146	47	193	76	24	3·17
2–13 April	565	297	862	66	34	1·90
30 April–4 May	202	160	362	56	44	1·27
7–11 May	188	166	354	53	47	1·13
			A. lineatus			
2–13 April	187	105	292	64	36	1·78
30 April–11 May	84	101	185	45	55	0·82
			A. sputator			
5–13 April	251	229	480	52	48	1·10
2–11 May	146	244	390	37	63	0·60

emerged in quantity and caused an inversion in relative abundance with *obscurus*. Over the same period a similar increase in the proportion of *sputator* occurred for the field as a whole. Evidently in this season *sputator* emerged relatively late.

(*b*) *In relation to sexes*

Table 5 is a summary of sex ratio data for all traps, and extends up to 11 May.

All three species showed a change in sex ratio (males/females) during the part of the season sampled. For *obscurus* the change from 3·17 to 1·90 (P 1–5%) was quite rapid, and occurred during the few days 3–5 April when a conspicuous emergence of *obscurus* was taking place, this being presumably relatively female. A further decline ($P<1\%$) was noticed during the latter half of April, but after that no change up to 11 May. The reason for this second decline is unknown. It was, however, well shown by *lineatus* as a decline from 1·78 to 0·82 ($P<1\%$) between the two periods 2–13 April and 30 April–

The enclosure consisted of a circular metal framework sunk 2 in. into soil and lined with cellophane, up which beetles could not crawl. Wheat plants provided food, and a piece of broken tile, shelter. The whole apparatus was kept in a small open glasshouse in which a continuous temperature record was taken. The recorder (Fig. 2) was designed to take advantage of the fact that beetles when active run up and down wheat stems. From an artificial stem of galvanized iron, a blade of thin copper spring ran at right angles; this, when depressed about 2 mm. completed a circuit powered by a dry cell in which an electric buzzer recorded on a smoked drum (diameter 3·5 in., 1 revolution per

week). Details of construction are shown in the diagram: it was necessary to have the recorder set in wax for rigidity, and the blade bent at right angles over a shallow bowl of mercury to prevent temperature variation in sensitivity. The copper spring was

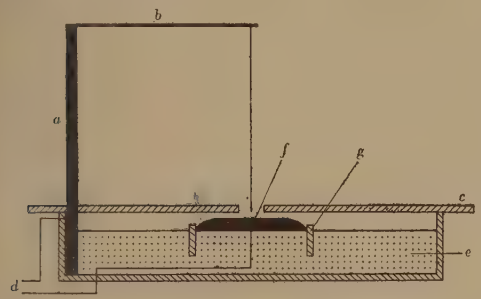

Fig. 2. Activity recorder. *a*, iron stem; *b*, copper spring; *c*, cardboard cover flush with surface of the soil; *d*, leads to electrical recorder; *e*, wax; *f*, mercury; *g*, glass ring.

after midnight to a low level by day. At night, activity showed considerable correlation

$$(r = +0{\cdot}437 : 1\text{–}5\,\%\ P)$$

with average temperature (mean 7·7° C.), and it is probable that temperature, which began to decline at sunset, often limited the amount of activity possible. Such a correlation ($r = +0{\cdot}497 : 1\text{–}5\,\%\ P$) was also shown during the morning (mean 10·2° C.), but not during the afternoon (mean 16·2° C.) or evening (mean 12·7° C.), indicating that temperature was limiting only during the night and morning when it was lowest. Another factor, hours of sunshine, affected morning activity and a good negative correlation ($r = -0{\cdot}477 : 1\text{–}5\,\%\ P$) was obtained with data supplied by the Meteorological Station at Rothamsted. No relation is shown at other times, and this may indicate either a low temperature sensitivity to light or an increased sensitivity after darkness. Fig. 3 illustrates the results obtained for a bright sunny day and a dull cloudy day.

The effect of cloud on these beetles has not previously received consideration. From these

Table 6. *Diurnal activity of* Agriotes obscurus (11 *May*–1 *June* 1946)

	Daily periods (G.M.T.)			
	Morning, 06.00–12.00 hr.	Afternoon, 12.00–18.00 hr.	Evening, 18.00–24.00 hr.	Night, 00.00–06.00 hr.
Sum of excitations for 22 days (SX)	24	47	123	85
$S\sqrt{x}$*	21·62	28·36	50·00	39·74

Standard error of transformed* sum differences = 3·85.

Analysis of variance

Source of variation	Degree of freedom	Sum of squares	Mean square
Total	87	57·140	—
Days	21	14·585	0·695†
Periods	3	21·392	7·131‡
Error	63	21·163	0·336

* A square root transformation was employed.
† Indicates that the mean square value is 1–5 % probable.
‡ Indicates that the mean square value is less than 1 % probable.

so adjusted that several quiescent beetles were unable to effect circuit closure, but one beetle moving about or dropping off caused a sufficient disturbance.

The results of a continuous record over 22 consecutive days in May are shown in Table 6. Each day was divided into four 6-hourly periods.

This reveals an appreciable amount of day-to-day variation in activity; but the major variation was diurnal. No simple statement, such as that they are nocturnal, is adequate; but it is quite clear that activity was greatest during the evening, inclining

studies it appears to influence them by day—affecting light intensity particularly on exposed arable fields—and by night—reducing radiation and thus prolonging the warmth of the day.

(2) *Flight*

The circumstances which induce flight appear to be quite distinct from those associated with walking and feeding.

Flight cannot be of common occurrence in this country (for review see Cohen, 1942) and evidence from various Russian sources appears to be con-

flicting or unsatisfactory because of the absence of climatic data—possibly flight is not regarded as a problem in Russia. However, Masaitis (1929), discussing flight of Elaterids in Siberia (Novo-Sibirsk region), mentions that beetles of the genus *Agriotes*

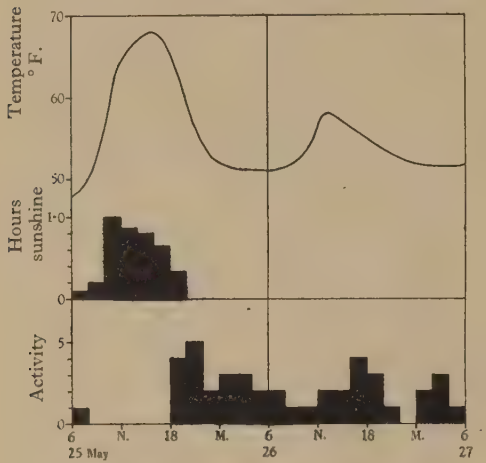

Fig. 3. Temperature, hours sunshine, and the activity of *Agriotes obscurus* on a warm sunny day, and a cool dull day (25 and 26 May 1946).

are protracted fliers (on the wing for a period of several months), but that their flying is feeble compared with that of *Selatosomus latus* F. and *S. pretus* Mannh. He mentions that *Agriotes obscurus* and *A. lineatus* fly, and that *A. sputator* flies at twilight from the end of May to the end of July. From his meteorological data it is evident that the temperature exceeded 20° C. throughout the day and occasionally rose to 27° C. at noon, and that the relative humidity exceeded 30% and rose to 58% as darkness approached. At this time of year in the vicinity of Novo-Sibirsk the climate during the day is steady, hot and humid—a climate quite unknown in Britain.

In this connexion certain observations on beetles in a glasshouse at Rothamsted are of interest. Beetles of all three species were kept in glass or cellophane cages on soil in which wheat was germinating. The tops of the cages were covered with muslin. Both sexes of *Agriotes obscurus* and *lineatus* were seen to fly frequently and regularly, but no *sputator*. *A. obscurus* proved a strong flier, more so than *lineatus* and if allowed, would fly about the glasshouse alighting when it made a contact. A beetle 'wanting' to fly was an unmistakable sight: it ran about actively and climbed wheat blades. On reaching the top of such a blade, if it could find a firm stance for its feet, it would open its elytra, spread its wings, pause a few seconds, and then start flying. At first it often fell to the ground, but after several attempts, it maintained itself in the air with success unless it bumped into something, when it settled and ran about seeking another point from which to take off. This behaviour would continue for several hours and be repeated several days in succession.

Eventually flying ceased, but that this was associated with the growth of gonads seems unlikely since specimens of *A. obscurus* with fully developed gonads, taken from the fields on 3 May, flew vigorously when placed in the glass cages—at a time when other beetles taken from the field earlier had ceased to fly. Considerable variation in the proneness to fly in favourable conditions was shown, which had no discernible relation to sex or age: certain individuals could be relied upon to fly regularly, others were never seen to fly.

Flight was noticed on the afternoons of hot sunny days in the closed glasshouse where wind was absent and humidity high. A *lineatus* female collected from the field in January and kept at laboratory temperature flew in the glasshouse on 15 March. Attempts to induce flight at night by raising the temperature to 20–23° C. were unsuccessful. The beetles would not fly in dry air. In general, as far as could be ascertained, *obscurus* and *lineatus* flew only when the temperature exceeded 21° C., provided the humidity was 80% or more and there was normal light or sunlight. It is possible also that the density of beetles in the culture, which was greater than would normally be encountered, was a factor stimulating flight.

However, it is probable that the rareness of flight in Britain is the consequence of a climatic deficiency and is not due to an innate deficiency in the beetles, since by simple manipulation of their environment they may be induced to fly. Possibly flight occurs in this country on exceptionally warm days in spring in sheltered localities such as pasture enclosed by woodland or south-facing protected slopes; and it is interesting to note that in Britain Elaterids of the genus *Athous* and *Corymbites* fly on hot sultry days which are evidently not quite suitable for the flight of *Agriotes* spp. Clearly there is here a promising line for further investigation.

Summarizing the foregoing sections about activity, it may be suggested that the 'ideal' climate for these beetles is one having a hot, still, sunny afternoon (for flying) which becomes cloudy at sunset (for feeding all night), and remains so with slight showers the following morning (for intermittent feeding and resting).

(*b*) *Movement*

Ghilarov (1941) has shown that in the vicinity of Moscow beetles of the species *A. obscurus* and *lineatus* are able to show distinct preferences for

certain types of crop, being much more common on plots of rye, for example, than plots of flax. These plots were quite large (180 m. square) in relation to the possibilities of walking, and as his total area investigated—two adjacent fields of eight such plots in all—was large, it is difficult to believe that the beetles developed this distribution without flying. However, as flying is certainly not common in Britain, it is of interest to know what movements a beetle can make by merely walking. Earlier in this paper, as a result of a simple calculation from trapping and sampling results, it was found that beetles which entered traps need only have travelled 1 yd. on the average. Gough & Evans (1942) have given evidence of beetles walking up to 30 yd. in a few days in thinly sown wheat; of moving across a path 4 yd. wide; and across 11 yd. of fallow. These workers used painted beetles which were later recaptured in grass traps.

A new method has been devised for tracing the movements of selected individual beetles. The chosen beetle, discovered by searching amongst the grass or under clods is marked with a small quantity of radium sulphate and replaced. Thereafter its location is discovered by examining the region about its last known position with a Geiger-Müller electronic discharge tube which detects and localizes the gamma radiation.

A very convenient tube powered by cable from the ordinary a.c. mains has been developed by Mr G. A. R. Tomes. It has the advantage of operating a loud-speaker directly without valve amplification; of quiet background, high sensitivity, and stable operation, and forms a compact, robust instrument for field use.

In this study only *obscurus* females were used. 5 μg. (5×10^{-6} g.) of radium sulphate sandwiched between thin aluminium foil disks 2 mm. in diameter were inserted with resin adhesive under the elytra. The whole insertion weighed only 2 mg. (average weight of female *obscurus* = 36·12 ± 0·31 mg.) and did not give the appearance of incommoding the beetle at all. Beetles so marked lived for apparently normal periods; the material had no direct contact with the body, and such knowledge as is available about the affects of gamma radiation on adult insects indicates that it merely increases the mutation rate by a small percentage. However, it is acknowledged that detailed studies of the effect on beetles have not been made, and at the present stage it is only possible to assess the value of the technique on the assumption that the marked beetle is not appreciably affected.* The quantity of radium sulphate used is sufficient to locate the beetle through 3 in. of soil—quite adequate, as they rarely leave the surface. Its position can be found to 2 in. though the beetle is invisible; and this enables the paths of individuals to be followed continuously if desired, throughout their life, with only the preliminary disturbance of marking.

The movement of three *obscurus* females was studied in permanent pasture during May and early June. The pasture herbage, about 6 in. high, contained the following species: predominantly *Lolium perenne*, *Cynosurus cristatus*, *Poa trivialis*, *Alopecurus pratensis*, and *Trifolium repens*, with a few scattered *Dactylis glomerata*, and *Ranunculus acris*.

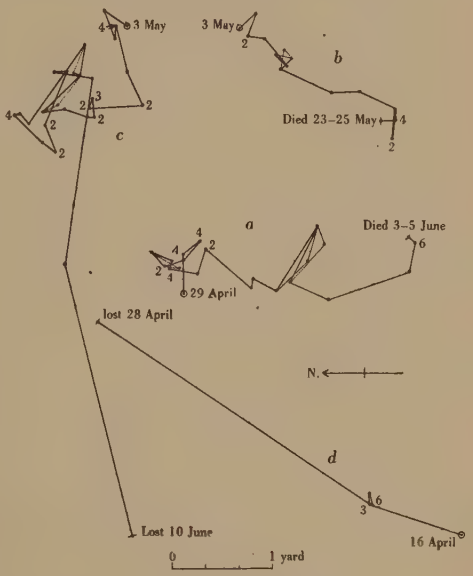

Fig. 4. Movements of female *Agriotes obscurus*: *a*, *b*, *c*, in pasture; *d*, in barley 2–3 in. high. Small numerals indicate the number of days for which a beetle was found in one position. Dotted lines join a few recorded afternoon positions.

The females were discovered about 6 yd. apart: Fig. 4*a*, *b*, *c* shows their position each morning and in a few cases in the afternoon. Evidently movement was not on a large scale. They were often found in the same place for several days in succession, but this was not due to climatic inhibition, as when one stayed still the others often moved. Changes in position up to 1 yd. occurred, again without correlated movements of the other beetles. Large movements of this order were generally followed by a relapse to small wanderings, and after 20 days (4–24 May 1946) the results could be summarized as follows (Table 7).

* Mr G. A. R. Tomes, *Twentieth-Century Electronics*, London, the designer of the tube, states that he has had similar disks attached to queen honeybees for several years with no apparent ill-effect.

Table 7. *Movement of three* Agriotes obscurus *females*

Beetle	No. of days on which no change occurred	Av. distance (in.) per day (Only moving-days counted)	Range	Net change of position
A	7	12	3–28	35 in. S.S.W.
B	6	8	3–20	59 in. S.W.
C	9	12	3–30	15 in. W.N.W.

It was then thought that, at any rate in permanent pasture containing an abundance of food and shelter, the females merely wandered about feeding here and there within a yard or two of their place of emergence. And beetles A and B died 6 ft. 11 in. and 5 ft. from their starting-points respectively.

This later proved to be not completely true however: a third type of movement was discovered. Beetle C (after A and B were dead) began on 6–7 June a large-scale directional movement, travelling 68 and 98 in. in a westerly direction. It had moved 5 yd. in 3 days, and on the fourth day it moved out of range. Movements of 38, 0, 27, 7, 53, 0 and 16 in. had been shown by another experimental beetle from 24 to 30 April: and one record from a field of barley (plants 2–3 in. high) showed a similar large-scale directional trend (Fig. 4*d*) from 17 to 27 April.

Summarizing the results of this season's observation, the beetles showed three types of movements: (*a*) They were found in the same place for several days in succession, always near the soil surface. (*b*) Much movement was of only a few inches and caused the beetle to wander about both by day and by night within an area of 2–3 sq.yd. (*c*) Large movements of several yards on successive days showed directional trend, and occurred occasionally.

4. NUTRITION

From the foregoing sections it appears probable that large numbers of beetles are unable to leave the field into which they emerge in spring. Consequently, it is of interest to know what effect the various farm crops are likely to have on the life and reproduction of these. Not only this, but the varied floristic composition of grassland, if sufficiently persistent in pattern, may, by influencing the quantity of progeny, bring about considerable differences in *Agriotes* distribution and density as long as their mobility is low or their preference high. Plants do not only affect beetles nutritionally, but they form shelter of varying quality, and by their reaction on the soil surface they affect the depth and ease of oviposition. The beetles feed on green leaves or on potato tubers or other vegetable matter by mashing the tissue with pronged mandibles and expelling a brown digestive juice containing protease but probably no cellulase.* The semi-digested pulp is then sucked, probably through a coarse filter formed by the maxillae, into the gut.

An experiment was designed to test the effect of various common farm crops and grasses on the numbers of progeny produced by *A. obscurus*. The beetles were fed throughout their active lives on a single crop, and at death the eggs were separated from the soil by a flotation method. As it was not known whether all the eggs collected were fertile, nor whether infertile eggs could survive several weeks in damp soil, it cannot be stated precisely whether fecundity or fertility was measured. At the same time, interesting observations on longevity and live weight were recorded.

Description of experiment

Eight plants were tested: *Agrostis tenuis*, *Festuca ovina*, *Lolium perenne*, red clover (late flowering), mustard, flax, wheat and potato (early). They were grown in waxed cardboard cartons, 3 in. in diameter on which was a lamp glass 6 in. high, widening out to 4½ in. near the top which was covered with muslin. Seeds were sown or tubers planted at an appropriate time in March and the plants brought to a suitable condition in a warm glasshouse by 1 April. The soil used had been dried to kill predators, and extended 2 in. up the lamp glass. Thus, a roughly cylindrical space 4 in. high and 4½ in. in diameter was left for the plants, which were watered by injection through a hole at the top of the carton to prevent the flattening and caking of the surface which follows from top watering.

Eight replicates of each crop were used, and the plants set out in a Latin Square in an insectary.

The beetles were then collected from the field (Stackyard) which, as already mentioned, was without vegetation at the time, and they could have eaten very little. Each was weighed and marked individually with paint on the protergum. Three males and three females (distinguished by examination of the external genitalia) were placed in each pot on 1 April 1946. Thereafter until the end of the experiment

* For this information I am indebted to members of the Biochemical Department, Rothamsted.

each pot was watered and examined weekly, the beetles always being discovered on or near the surface.

As far as could be ascertained, egg-laying began in the first week of May; in the second week the males began dying on flax and potato in considerable numbers. Records were kept of the week in which each individual died. Dead females were dissected and the eggs inside counted. At the end of the experiment it was possible to conclude that females dying by accident (commonly by being stuck on their backs with water to the glass side of the vessel) might contain many eggs—up to 147—but females dying 'naturally' rarely contained as many as five eggs, but often one or two. Most of the accidental female deaths occurred relatively early, and the number of eggs found in all dead females was added to the total found later in the soil of that pot.

The first larvae were found in pots examined on 18 June. On 21 June, to avoid reduction of progeny by cannibalism, all the plants and living beetles in pots which were still productive were transplanted successfully to new pots and fresh soil, and the old ones examined for eggs and larvae.

Results of experiment

(*a*) *Live weight*

The live weights of *Agriotes sputator*, *lineatus*, and *obscurus* at the beginning of the active season in late March are shown in Table 8.

In all cases average male weight was less than average female weight, although considerable overlap of the frequency distributions occurred. The difference in sex mean weight increased with species mean weight, as did also the standard deviation.

Table 8. *Live weights* (*in mg.*)

	A. sputator		*A. lineatus*		*A. obscurus*	
	Mean	Standard deviation	Mean	Standard deviation	Mean	Standard deviation
Males	13·77 ± 0·20	1·98	26·23 ± 0·34	3·40	30·22 ± 0·24	3·38
Females	14·49 ± 0·23	2·27	28·44 ± 0·37	3·65	36·12 ± 0·31	4·37
Difference	0·72	—	2·21	—	5·90	—
Significance of difference	1–5 % *P*	—	< 1 % *P*	—	< 1 % *P*	—

Determined from 101 males and 101 females in *sputator* and *lineatus* and from 204 males and 204 females in *obscurus*.

As soon as all the females in a pot were dead, the soil (in lamp glass and in carton separately) was examined for eggs and young larvae. Without pretreatment it was gently disintegrated with a fine spray of aqueous magnesium sulphate solution (specific gravity, 1·18); roots were carefully washed in the same way, and the whole material transferred to the flotation apparatus described by Salt & Hollick (1944). The surface material was collected on 0·1 mm. mesh bolting silk after the usual blowing, stirring, and settling operations. It was then washed out in water, and the eggs, which sank to the bottom, removed and counted with a pipette. The remainder was treated with xylene and examined for small larvae by the method described by Salt & Hollick.

Most of the progeny (eggs and larvae) were found in the top section of soil, but the numbers found in the bottom section were not negligible, and might amount to 12 % of the total. In one case in a pot of flax 82 out of 126 were found in the bottom, but this was quite exceptional. Although the soil was loose and crumbly most eggs were laid within 1 or 2 cm. of the surface, the females making no attempt to burrow, but merely inserting their extended ovipositor down small crevices. Probably they would have behaved otherwise if the surface had been dry.

At that time both sexes had a considerable fat body, but the gonads were poorly developed. It was not until the last week of April that, in specimens collected from Stackyard, eggs were present in the ovary and the testes were well developed. There was still a large fat body. From that time onwards, however, whilst egg-laying was proceeding, the fat body dwindled and was quite absent from specimens dying a 'natural' death: only the empty gonads were left. (This applies to all three species.)

On 20 May in the middle of the oviposition period the experimental *obscurus* females were weighed again and their individual weight changes since 1 April recorded. Table 9 shows the results obtained.

They range from increase through no change to loss in weight. *Agrostis* and *Festuca* show a very slight but significant (1–5 % *P*) increase; clover and *Lolium* do not show significant change; wheat, mustard, flax and potato all show decrease in significantly different degree. These figures will be related to fecundity later on.

(*b*) *Longevity*

Longevity is measured from 1 April, which may be taken to represent only a slight under-estimate of the duration of active adult life. However, it is not as a precise measure of longevity that this experiment

was designed, but to give comparative results much more useful in ecology. In common with many other beetles, female *Agriotes obscurus* live longer than males, and this difference was sufficiently marked to necessitate the separate treatment of sexes. The results are set out in Table 10 and survival curves drawn in Figs. 5 and 6 (of which the original details are deposited for reference at Rothamsted).

Table 9. *Change in weight (mg.) of* Agriotes obscurus *females from 1 April to 20 May on various crops*

Crop	Nos. weighed on later date	Mean change in weight	Change as percentage initial weight
Potato	21	−4·80	13–14
Flax	23	−3·39	9–10
Mustard	22	−2·01	5–6
Wheat	22	−0·90	2–3
Clover	21	−0·59	0
Lolium	20	−0·31	0
Festuca	24	+0·94	2–3
Agrostis	20	+1·07	2–3

Mean square for error = 2·405.

Table 10. *Longevity of* Agriotes obscurus *on various crops*

Crop	Mean age from 1 April (days)	
	Males	Females
Flax	45·9	69·0
Potato	47·7	64·2
Mustard	53·5	78·1
Wheat	55·1	67·1
Agrostis	61·1	75·4
Clover	64·3	76·2
Lolium	66·4	81·0
Festuca	75·4	83·9
S.E. of mean difference	3·40	4·05

Pronounced and statistically significant variations in age are shown. The sexes correlate broadly in this respect, but some outstanding exceptions are worthy of notice: females lived very long on mustard, and the difference in age of the sexes on flax is very large. However, these differences in sex mean age are not statistically significant. Three distinct longevities are discernible amongst the males: (1) flax and potato, (2) *Agrostis* and clover, and (3) *Festuca*, with the other crops falling in intermediate positions. Amongst the females, potato, wheat and flax, indistinguishable amongst themselves, are distinct as a group from *Lolium* and *Festuca*. Other differences between pairs of crops will be noticed.

A feature of interest in the survival curves, is that although death began at approximately the same time on all crops it proceeded more rapidly on unfavourable ones, and extended over a long period on favourable crops. This is easily seen in the death (*d*)

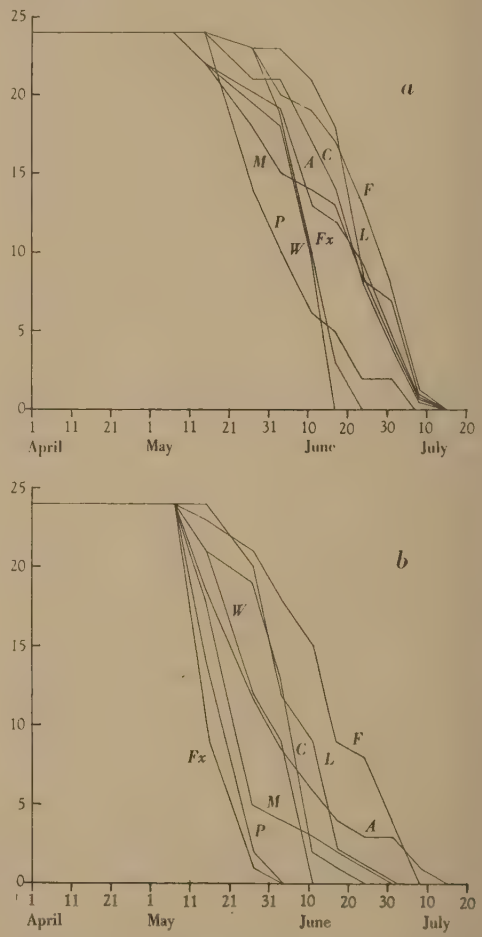

Fig. 5. Survival of *Agriotes obscurus* L. (*a*) females, (*b*) males on eight crops: flax (*Fx*), potato (*P*), mustard (*M*), clover (*C*), wheat (*W*), *Agrostis tenuis* (*A*), *Lolium perenne* (*L*) and *Festuca ovina* (*F*).

histograms for both sexes on flax and wheat on the one hand, and *Lolium* and *Festuca* on the other (Fig. 6). Pearl & Miner (1935) have shown similar differences between the survival curves of starved and fed strains of *Drosophila*. In both *Agriotes* and *Drosophila* nourishment, besides increasing mean longevity, also increases variance.

(*c*) *Progeny*

These results, expressed as progeny per female for each crop, are shown in Table 11*a*, col. 1. An analysis of variance after the data had been suitably transformed showed that both rows and columns of the Latin square had significant variance, which illustrates the necessity for such design in an experiment of this kind.

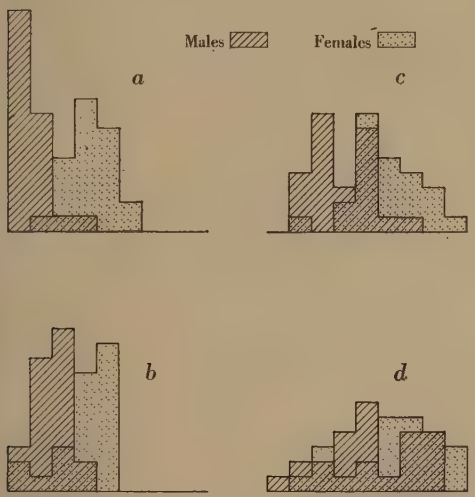

Fig. 6. Death frequency histograms for *Agriotes obscurus* L. on (*a*) flax, (*b*) wheat, (*c*) *Lolium perenne*, (*d*) *Festuca ovina*.

Crop variance was very significant (< 1 % *P*). It was further found that a significant reduction in error mean square could be effected by covariance analysis of the data with the weight of females in each pot at the beginning of the experiment. Hence progeny and weight of females were correlated within crops, heavy females producing on the whole more eggs than light females. But no correlation between these factors existed in respect of crop means and, consequently, after adjustment of these (progeny means) for variation in weight of females, their variance remained highly significant (< 1 % *P*).

In col. 4 of the table, transformed adjusted progeny means are given, and a mean standard error of differences suitable for their examination is supplied below. Compared with col. 2 it is seen that the changes are only small, and no difference in array is caused. In col. 5 these are reconverted into normal adjusted crop progeny means.* Flax was manifestly worse than any other crop except potato. About five times as many eggs were laid on *Agrostis* which was closely approached and statistically indistinguishable from *Festuca*. Very interesting is the significant difference between *Lolium* and the other two grasses. Wheat, again, was significantly different from *Lolium* and it is quite clear that graminaceous plants had very variable effects on progeny. Potato, clover and mustard were indistinguishable from wheat, but mustard was better than potato.

Summary of experimental results

The results are summarized in Table 12.

It is now possible to see that the change in live weight of females from 1 April to 20 May was very closely related to progeny. The probable explanation of these results is that active egg-laying on nourishing foods is accompanied by a slight average increase in weight, but that on less favourable foods egg-laying is at the expense of the fat body, the transposition of whose material occurs later and later, in proportion to the nutritive value of the crop. If the weight of one egg is taken to be 0·1 mg. and it is assumed that all the eggs laid have been recorded, females on *Agrostis* laid 39 % of their initial weight, whereas on flax they laid only 7·5 %. The smallness of these figures suggests the possibility that a considerable portion of the fat body is respired if the crop is unfavourable, and it may be noticed that the loss in weight on flax and potato by 20 May exceeded the weight of eggs laid in the whole season (2·70 and 3·47 mg.). But it should be recalled that infertile eggs may have been laid and subsequently decomposed by soil organisms. Fecundity is thus dependent upon larval nutrition (initial weight regression) and adult nutrition.

The relation between longevity and progeny was not so close as the foregoing, and certain exceptions are worth noticing. Mustard and clover may be described as crops on which beetles survive well but lay few eggs. On *Agrostis*, on the other hand, they produce many eggs, but do not live any longer. The reasons for these disparities are unknown.

No longevity regression on initial weight could be detected.

5. DISCUSSION

The main theme of this paper has been an inquiry into the habits, distribution, and reproduction of *Agriotes* spp. in their normal habitat, and some attempt has also been made to assess the chance of survival and reproduction should that environment be abruptly changed by cultivation. It is quite

* Owing to the nature of the logarithmic process these figures are not as useful absolutely as those of col. 1—it will be noticed that they are all smaller than their corresponding figures—but, relatively, that is, as comparisons of plant effects they are better, because they have been adjusted for unavoidable variations in weight of females.

evident, as Miles & Cohen (1939–40) have pointed out, that grassland is the best habitat, not only by virtue of its stability, and the multiplicity of its protective effects, on both adults and larvae, but on account of its effect on the number of progeny produced by each generation of adults. Apart then from the exposure of the *Agriotes* population to predation, desiccation and mechanical injury which the cultivation of grassland entails, the usual result is a deterioration in food resources due to the planting of one of the usual farm crops. The effect here is not simple, however, for Evans (1944) has shown that certain foods (wheat, carrots and onions) are better than grass for promoting growth of larvae. But even if one of these crops were planted and the larvae suffered no check, the population would decline slowly owing to the diminished fecundity of those adults which did not move away. Clearly to effect rapid decline without resource to one of the several potent insecticides recently discovered, flax is the most suitable crop, causing as it does a loss in dry weight of larvae, and a very small progeny production by females.

Table 11*a*. *Progeny per female* Agriotes obscurus

Crop	Mean progeny (per female) Normal	Mean progeny (per female) Transformed* X	Mean weight of females (per pot) Y	Progeny means adjusted for regression on weight: Transformed	Progeny means adjusted for regression on weight: Normal
Flax	30·7	1·919	109·1	1·906	27·0
Potato	36·2	1·996	105·4	2·018	34·7
Wheat	50·3	2·141	105·9	2·159	48·0
Clover	61·2	2·244	112·1	2·202	53·0
Mustard	63·8	2·216	105·4	2·239	57·7
Lolium	81·8	2·374	104·1	2·409	85·3
Festuca	146·0	2·625	111·7	2·587	128·7
Agrostis	149·0	2·629	108·2	2·625	140·7

Mean standard error of difference between transformed adjusted means = ±0·0797.

* A logarithmic transformation of progeny was used.

Table 11*b*. *Analysis of covariance* (*progeny on initial female weight*)

Source of variation	Degrees of freedom	Sy^2	Sxy	Sx^2	Error of estimate	Degrees of freedom	Mean square
Total	63	3341·80	49·738	5·8476	—	62	—
Rows	7	458·51	10·850	0·3683	—	6	—
Columns	7	321·40	6·391	0·3759	—	6	—
Crops	7	517·04	12·716	3·9074	3·5947	6	0·5991*
Error	42	2044·85	19·781	1·1960	1·0046	41	0·0245
Crops plus error	49	2561·89	32·497	5·1034	4·6912	48	—
For testing adjusted treatment means					3·6866	7	0·5267*

* Indicates that the mean square value is less than 1% probable.

Table 12. *Summary of experimental results*

Crop	Adjusted progeny per female	Female loss in weight by 20 May	Male longevity (days)	Female longevity (days)
Flax	27·0	−3·39	45·9	69·0
Potato	34·7	−4·80	47·7	64·2
Wheat	48·0	−0·90	55·1	67·1
Clover	53·0	−0·59	64·3	76·2
Mustard	57·7	−2·01	53·5	78·1
Lolium	85·3	−0·31	66·4	81·0
Festuca	128·7	+0·94	75·4	83·9
Agrostis	140·7	+1·07	61·1	75·4

It has been shown that grasses themselves are of variable value to the beetle; and it is fortunate that of the three grasses studied the two most satisfactory for the beetle are considered least desirable by the farmer. Salt & Hollick (1946) have shown for a population of *Agriotes sputator* a pronounced positive correlation between the density of larvae and the percentage of *Agrostis stolonifera* on the sample, and a negative correlation between density and the percentage of *Lolium perenne*. Although the results presented in this paper relate to different species of beetle and plant, comparison may not be unprofitable. The abundant small larvae characteristic of Spinney Pasture must have played an important part in establishing the correlations mentioned. Moreover, in the same pasture, Salt & Hollick have shown the distribution of this size class to be distinctly aggregated, presumably as a result of ovi-

position in batches. It is thus tempting to suppose that one of the factors affecting their distribution was the difference in reproductive capacity (perhaps further emphasized by active preferences) of the beetles in relation to the two plant species *Lolium* and *Agrostis*. Although *Festuca ovina* has been found to be a favourable food for adults, Salt & Hollick found no correlation with its distribution in spinney pasture—where, however, it occupied only 2% of the area over samples.

It thus appears that, did the character of the vegetation alone determine the density of an *Agriotes* population, the vegetation of hillside pastures (*Agrostis-Festuca* grassland on acidic soils, and *Festuca* on alkaline soils) would prove more favourable to *Agriotes obscurus* than the vegetation of permanent pastures and leys where *Lolium perenne* tends largely to replace the other two. However, it may be the residue of agriculturally undesirable grasses which enables wireworm populations to exist at a high level of abundance in these places, and perhaps further development of ley farming and selection of seed mixtures may lead to a gradual reduction of numbers. The value in future work of paying attention to the population of *Agriotes* in relation to the various ecological types of grassland as well as to the study of the effects of various common species of grass as foods for both larvae and adults is amply demonstrated.

A number of interesting differences between the species have been brought to light. These, as pointed out earlier, tend to reveal a divergence of *sputator* from the other two in habits as well as size and form. Thus, the various differences between mean sex weights, the later emergence of *sputator* from the soil in spring, the varying behaviour of trap-catches in relation to daily climatic fluctuations, together with the generally reduced proportion of males in *lineatus*, and (more so) in *sputator* as compared with *obscurus* at equivalent times in the season may be recalled. Also, it has been mentioned that *sputator* was not seen to fly in conditions quite suitable for *lineatus* and *obscurus*.

6. SUMMARY

1. The beetles *Agriotes obscurus* (L.), *A. lineatus* (L.) and *A. sputator* (L.) on freshly ploughed old pasture land showed distinct differences in spatial density distribution, even between areas only 15 yd. apart. Day-to-day variations in catch showed good correlation between all three species, but on good days *sputator* tended to increase relative to the others.

2. Emergence from the soil occupied a period of about 3 weeks, *sputator* emerging later than the other two species; within species, the males appeared earlier than the females with considerable overlap, but the ratio males/females declined, not gradually, but in stages, during the early part of the active season. At any particular time the species *obscurus* contained more males than *lineatus*, and *lineatus* more than *sputator*.

3. By means of an automatic recorder in an insectary, the activity of *A. obscurus* adults was studied, and it was found that activity at night (midnight to 06.00 hr.) was positively correlated with temperature; and in the morning (06.00 hr. to noon) positively correlated with temperature and negatively with hours of sunshine. Most activity was shown in the evening: it is suggested that cloud is an important factor in the beetles' life.

4. The flight of *A. obscurus* and *lineatus* was observed regularly in a warm humid glasshouse in March, April and May.

5. Studies of movement by walking in grassland by means of a new electronic detector method have proved practicable and have so far supported the idea suggested by various lines of evidence that beetles are relatively sedentary, although there were indications of larger directional movements as well.

6. The live-weight distributions of both sexes of the three above-named species of *Agriotes* at the beginning of their active season were measured. In all cases males averaged less than females with considerable overlap, the difference increasing with mean species weight.

7. The small changes in live weight which ensued in *A. obscurus* are discussed in relation to the environment of a pot experiment in which eight crops were tested for their effects on fecundity and longevity. This experiment showed that on three grasses, *Lolium perenne*, *Agrostis tenuis*, and *Festuca ovina*, more progeny were produced than on mustard, wheat, flax, clover and potato; but *Lolium* yielded less than the other two grasses. Flax gave lower yields than all except potato. On the whole the heavier females laid more eggs.

8. Females lived longer than males in all cases and, in general, longevity was greatest where progeny was greatest, but notable exceptions occurred. It was also found that death of the population extended over a brief period on unfavourable crops and over a longer period on favourable ones.

ACKNOWLEDGEMENTS

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A NOTE ON *CROCIDURA RUSSULA* AND OTHER MAMMALS IN ALDERNEY, CHANNEL ISLANDS

By LEO HARRISON MATTHEWS

Two species of shrew live in Jersey, *Sorex araneus fretalis* Miller the local subspecies of the common shrew, and *Crocidura russula* (Hermann) the musk shrew. Morrison-Scott (1937) brings forward evidence suggesting that in this island *Crocidura* is confined to the neighbourhood of the shore and *Sorex* occupies the inland localities. He points out that on the continent *Crocidura russula* has a uniform distribution in France.

The writer of the present note spent a fortnight trapping small mammals on the island of Alderney in August 1946, and found *Crocidura russula* fairly abundant in all localities from the seashore to the highest point. The island is $3\frac{1}{2}$ miles from north-east to south-west, the average breadth is 1 mile and the area 1962 acres. At least in this island, therefore, the species has not a differential distribution. It is, however, the only shrew on Alderney, species of *Sorex* being absent.

The breeding season on this island is evidently prolonged, for during the second half of August females were obtained containing early and late pregnancies, and a nest of half-grown young was found in a cornfield on the summit above St Anne.

The other mammals found on Alderney were: *Apodemus sylvaticus* (L.), common everywhere, breeding in August; some specimens very large, up to 107 mm. in head-and-body length. *Mus musculus* L., both on the shore and on the summit away from houses. *Rattus rattus* (L.), one juvenile specimen, St Anne. *Rattus norvegicus* (Berkenhout), the mummified remains of several animals found in the fortifications and dug-outs of the recent war. *Oryctolagus cuniculus* (L.), present and widespread but not very common. *Talpa europaea*, 'heaves' in several fields round St Anne, and even in a garden in the town; abundant at the south-west end of the island. Several small bats were seen at dusk flying round the farm buildings above St Anne, and near ruins at Crabby Bay, but it was not possible to identify them.

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REVIEW

PREDATOR-PREY RELATIONS

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A charge often levelled against animal ecology by more 'academic' zoologists is that the subject is really no more than glorified natural history.

Even if this were true, there would be much to be proud of in the title, but the lack of precision which is charged against ecology is rapidly passing. Quantitative studies made during the last 10–15 years on autecological lines have not only given us critical pictures of the turnover of many species—in other words have attempted to construct life tables for wild animals—but have allowed us to draw important generalizations about the behaviour of populations. We have begun to know how the productivity of an animal is related to its expectation of life; how the incidence of mortality is distributed over the age groups; how density may vary in different periodicities or without periodicity at all; we see that wild populations have certain capacities for self regulation and so on.

Thus a body of precise, demographic fact is spreading from the focal points of species studies (we will not mention the vast mass of work upon techniques which has been needed to enable such measurements to be made upon wild populations).

Along with this has grown a body of mathematical work treating mainly of the theoretical effects of competition between parts of an animal community. One important aspect of this deals with the control of numbers by competition for limited environmental resources or the mutual adjustment of predator-prey relationships. Given certain conditions of environment and of efficiency in using that environment (for reproduction and feeding) certain theoretical relationships between predator and prey can be forecast—for instance, the point where the increase of the prey is just cancelled by the requirements of the predator, the latter being conversely limited by the availability of the prey (the steady state). Many other fundamental relationships may be inferred.

The lines opened to experiment by such work have so far mainly been confined to laboratory work, in which the barest bones of a competitive relationship are studied (e.g. work on *Tribolium*). It is fair to say that the theoretical expectations have in part been fulfilled, but the problem of whether such fundamental properties of populations are really exhibited under the intricacies of a wild animal community is much more difficult to examine. To work out quantitatively the balance of a complete community is impossible with present resources, nor has theory yet suggested what is to be expected in such conditions. Even the measurement of a predator-prey relationship in nature is complicated because few predators available for study are monophagous. Furthermore, it is difficult to determine when a prey species is likely to be controlled by one predator. The only available method is to choose a relationship which appears to approximate as nearly as possible to the ideal condition of the watertight compartment.

The present paper on the sparrowhawk (*Accipiter nisus*) as a predator on four species of passerine birds in Holland, is the first attempt to study quantitatively the relationship between predator and prey in a wild vertebrate population. Its aims are limited, so that only an approach is made to the fundamental problem of whether the sparrowhawk population controls those of the prey species, while at the same time being limited by them. It is made quite clear that the work was undertaken to discover whether *the sparrowhawk under the given circumstances was responsible for a substantial fraction of the total mortality suffered by the prey.*

It seems probable from the way in which the discussion develops that only during the work did the writer discern that the material and techniques evolved by him for treating it would yield information upon the more fundamental problems of population control. This final presentation of the results has been written with the limited objective only in view. Although actual population figures for predator and prey are available over three years, little attempt has been made to trace whether the mutual conditions of one year are derived from those of the previous one. In fact yearly variations are smoothed out: 'in this way I hoped to obtain during a short series of years values that approach the average state rather than the actual figures.' The writer has no doubt been wise so to restrict himself, though it seems a pity that the data should not be re-analysed with the further aim in view. The results would no doubt be inconclusive, but, since nothing of this kind is yet available, the author is rather forfeiting the credit of having been the first in this particular field. Naturally a series of data from more years would be needed to make a complete study, and it is to be hoped that, now the laborious task of working out the field techniques for such a study has been accomplished, the continuation of the work to finish what might well be a classical study will be ensured. Even if this is so, and certainly if it is not so, there would be great value in assessing how far the present data support the possibility that mutual control between predator and prey exists.

There are some points in the actual presentation which should be noted. The paper itself is long and not easy to assimilate (the Dutch text extends to 184 pages), but the long English summary (25 pages) and the addition of English legends to tables and figures are extremely helpful. The data are given very completely and, considering how difficult it is to write comprehensive papers of this kind, it is well held together. The main lines of argument are slightly obscured by the unavoidable discussion and explanation of techniques, so that some such device as using different sizes of print, or reassembling the main threads at intervals, would have been welcome. No use at all is made of appendices.

There are some features in the choice of material which militate against the possibility of testing the mutual interdependence of predator and prey. The sparrowhawk is migratory in Holland, so that the turnover of the breeding population may be partly controlled

by conditions away from the area of study. Again, the species of predator chosen has an average density so small (the breeding population varied from 1 adult to 1–2000 acres) that relatively vast tracts have to be investigated to give significant figures. Lastly 'super-predation' occurs, since some sparrowhawks are killed by goshawks (*Accipiter gentilis*). This last is very unfortunate. However, these factors, excepting the size of area to be investigated, do not militate so much against the limited objective set.

The general plan was to carry out intensive work upon an area of some 2600 acres with 5–9 adult sparrowhawks in the breeding season and to study a further 19,000 acres less intensively and to a certain extent by extrapolation from the smaller one.

The basic data required are the breeding population and productivity of the predator and of the four species of prey, the house sparrow (*Passer domesticus*), the chaffinch (*Fringilla coelebs*), the great tit (*Parus major*), and the coal tit (*P. ater*). From these the principal aim is to estimate the numbers of all present on the areas during May, the total mortality of all and the amount of the prey mortality due to sparrowhawk predation during the same month. For some of the prey species similar figures are also calculated for August and for the quarter June to September, but these are necessarily less accurate.

The methods of arriving at these data vary and some show unavoidable traces of extemporizing. Thus, the breeding stock of house sparrows is derived from sample counts giving the number of males per house, multiplying by the total of houses and then by the sex ratio (obtained from sample counts in November). Since a nest count of one area carried out later does not agree, a general correction of 10% is added to the census figures. However, the breeding population of the other three species is determined more simply from sample counts of singing males in all representative types of habitat.

Productivity figures (to give mortality on the assumption that the population returns to par at the start of each breeding season) are obtained for the house sparrow by August counts of the ratio juveniles: adults; for great tits from nest-box data (year specific but not locality specific); and for the coal tit from similar data which are neither year nor locality specific.

Mortality figures are derived from those above by assuming a constant monthly mortality rate throughout the year, except in the case of the chaffinch, where an average figure has been derived independently of productivity figures from ringing returns.

Similarly for the sparrowhawk the general mortality rate is arrived at from the mean productivity on the smaller and more intensively studied area. A correction has had to be made to eliminate the effect of the predation on young sparrowhawks by goshawks.

Finally the average number of each prey species taken by each sparrowhawk during May is found from (*a*) extensive data at plucking stations of the relative proportion of each species in the prey remains and (*b*) the rate of feeding at the nest observed during sample periods of watching.

This summary of the devious means employed in accumulating the basic data is given to emphasize (*a*) the urgency of fixing upon the simplest possible form of a problem in the field (enough snags will accumulate without inviting any in at the beginning) and (*b*) the value of pertinacity in arriving at a figure by roundabout or improvised methods, if the straight way fails.

Finally, this work impresses one with the desirability of relying, wherever human wit can devise it, upon data collected on the spot. In every case, where external data have been used, it is difficult to assess their applicability to the particular case studied. The approach to this sparrowhawk problem seems always to be hesitating between studying what is actually happening and what is the general trend of events underlying the observations. We are left with neither a clear narrative, nor a firm generalization.

To turn to the results: the proportion of each prey species taken by sparrowhawks is given as the amount per cent. of the total stock of each on the study area and as the amount per cent. of the total expected mortality of each species. For house sparrows during May on the smaller study area these figures are 3·6 and 34%; for the coal tit, 5·6 and 38%. Actually, since sparrowhawks hunt nearer their nests during May than in other months, a correction has been applied for this, making the figures: house sparrow, 8·4 and 79%; coal tit, 2·3 and 15%. For the other two species the comparable figures are: chaffinch, 2·6 and 30%; great tit, 5·7 and 44%.

The second figure of each pair shows that, except in the case of the coal tit, the sparrowhawk constitutes a very important part of their mortality, remarkably so for the house sparrow. On these figures the author's limited objective is amply demonstrated.

As regards the problem of mutual control there is a strong suggestion that three of the prey species may enter into this kind of relationship. For the house sparrow, chaffinch and great tit the census figures for the years 1941–3 show a general drop (up to and over 50%) in the second year with a substantial recovery (*c.* 25%) in the third year (Table 24). On the smaller area the stock of sparrowhawks declines throughout (Table 30). This is what might be expected, if the scarcity of prey during the second year were reducing the predator stock (either by decrease of breeding efficiency or by starvation), since, if a characteristic predator-prey oscillation is involved, the recovery of the prey in the third year would be ahead of a recovery in the predators. It may also be noted (Table 30) that in the middle year the productivity per nest of the sparrowhawks *was* reduced (1·6 young per nest compared with 2·3 in the previous year), though here the complication of goshawk predation upon the sparrowhawks enters. There is also the difficulty that there are no data to tell us what happens during the rest of the year, especially during the winter. These considerations, therefore, can only be regarded as holding out promise for future investigation on such lines.

The great service of this pertinacious piece of work is to have made a start in attacking the problem of vertebrate population control from a fundamental angle. One hopes that energy will be diverted now from the species study towards such an approach, and that the value of such 'pure' research (it is in essence laborious, expensive and time-consuming) will not be obscured by the attractions of ad hoc results upon animals of immediate economic importance.

H. N. SOUTHERN

NOTICES OF PUBLICATIONS ON THE ANIMAL ECOLOGY OF THE BRITISH ISLES

This series of notices covers most of the significant work dealing with the ecology of the British fauna published in British journals and reports. Readers can aid the work greatly by sending reprints of papers and reports to the Editor, *Journal of Animal Ecology*, Bureau of Animal Population, 91 Banbury Road, Oxford.

Duplicate copies of these notices can be obtained separately in stiff covers (printed on one side of the page to allow them to be cut out for pasting on index cards) from the Cambridge University Press, Bentley House, 200 Euston Road, N.W. 1, or through a bookseller, price 3*s.* 6*d.* per annum post free (in two sets, May and November). Back numbers are available at half price.

Selection and abstracting has been done voluntarily by H. F. Barnes, R. H. Clarke, A. C. Evans, P. A. Larkin, E. M. O. Laurie, E. Nelmes, F. T. K. Pentelow, W. S. Richards, M. R. Shorten and H. N. Southern; checking by B. M. Hobby.

Within each section the groups are arranged in alphabetical order. Papers dealing with technical methods are dealt with in the appropriate sections.

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1. ECOLOGICAL SURVEYS AND THE RELATIONS OF ANIMALS TO HABITAT CONDITIONS

(*a*) Marine and brackish

Farran, G. P. (1947). 'Vertical distribution of plankton (*Sagitta*, *Calanus* and *Metridia*) off the south coast of Ireland.' Proc. R. Irish Acad. 51, B, no. 6: 121–36.

The vertical distribution of *Sagitta elegans*, *Calanus finmarchicus* and *Metridia lucens* sampled during a consecutive day and night in August 1931 and 1932 at depths of 100–125 m.

Jones, J. W. (1947). 'Salmon smolts and salt water: survival of smolts of *Salmo salar* at various rates of increase of salinity.' Salm. Trout Mag. (Lond.) no. 119: 63–76.

Smolts from the R. Dee were transported to Port Erin (Isle of Man) and transferred to sea water. An immediate change appeared to be fatal but when fresh water was replaced gradually by sea water the fish survived. There was a considerable increase in mortality after the fish were marked.

Lebour, M. V. (1946). 'The species of *Teredo* from Plymouth waters.' J. Mar. Biol. Ass. U.K. 26: 381–9.

At Plymouth there occur the two species of wood-boring lamellibranchs *Teredo norvegica* and *T. megotara*, and also a small variety of *T. navalis* whose taxonomy, larval development and metamorphosis are discussed. *T. megotara* is found in drifting wood only. The breeding of *T. megotara* and *T. navalis* var. takes place throughout the year at Plymouth, although there are spring and summer peaks.

McMillan, N. F. (1946). 'Some Cheshire amphipods.' Northw. Nat. 21: 102–3.

Records of four species of *Gammarus* and two of *Orchestia* collected in Cheshire in 1941–4. *G. zaddachi* and *O. mediterranea* are reported from this county for the first time and two additional localities are given for *G. tigrinus*, which was hitherto known from only two places in Cheshire. An unusual occurrence of *G. pulex* in a stream affected by spring tides is reported.

Wagstaffe, R., Williamson, K. & Broughton, R. H. (1946). 'The invalidity of some early records of Brünnich's guillemot in Britain.' Northw. Nat. 21: 20–6.

Of the three specimens of *Uria lomvia* found in Yorkshire in 1894–5 and accepted as the first authentic ones recorded from Britain, two certainly and one most probably should be referred to *U. aalge* in winter plumage; the identity of a fourth recorded from Cambridgeshire during the same winter and compared with them is also doubtful. Of the eight other British records, only three (from East Lothian, the Faroe Islands and Great Saltee) appear to be free from suspicion.

Yonge, C. M. (1946). 'On the habits and adaptations of *Aloidis* (*Corbula*) *gibba*.' J. Mar. Biol. Ass. U.K. 26: 358–76.

An eulamellibranch specialized for life in muddy sand mixed with gravel, at depths up to 80 fathoms. Admixture of gravel is important since the mollusc anchors to this by a single byssus thread thrown out after it has burrowed just below the mud surface. The siphons, ctenidia and stomach are specialized to exploit diatoms, bacteria and organic debris.

Yonge, C. M. (1946). 'On the habits of *Turritella communis* Risso.' J. Mar. Biol. Ass. U.K. 26: 377–80.

This gastropod buries itself in the mud and remains stationary for long periods. Observations show that probably it is exclusively a ciliary feeder, there being folds of the head region which form a functional exhalant siphon (unique in prosobranch molluscs) which is no doubt correlated with the mud-burrowing habit.

(*b*) Fresh water

Collinge, W. E. (1946). 'Notes on the British freshwater Isopoda, No. II.' Northw. Nat. 21: 31–5.

Contains descriptions of five new varieties of the water-louse, *Asellus aquaticus*; a check list of the British freshwater Isopoda; and records of *A. aquaticus* from 13 counties in Great Britain and from the Isle of Man, and of *A. meridianus* from 10 counties in England and Scotland.

Lloyd, Ll. (1944). 'Biological investigations in relation to incipient ponding.' J. Proc. Inst. Sewage Purif., 1944: 71–4.

A record is given of 1600 c.c. samples of washings taken from the medium at the sub-surface layer of a number of sewage beds at Knostrop, Leeds. Numbers of *Lumbricillus lineatus*, *Psychoda* larvae and pupae, and *Metriocnemus* larvae and pupae are given for each sample. The distribution of *Psychoda alternata* seems to be connected with the size of medium and not with the type of sewage, either because the smaller grade holds more film and deposit, which is favourable to the species, or because these conditions are unfavourable to *Metriocnemus*, a fly which is a direct controlling factor of *P. alternata*.

Lloyd, Ll. (1945). 'Animal life in sewage purification processes.' Paper read to the north-eastern branch of The Institute of Sewage Purification on 7 April 1945. 23 pp.

The animal life in percolating filters and in activated sludge systems of sewage purification is surveyed. The occurrence of the organisms in natural surroundings is also described. The role of Protozoa in the purification, and the behaviour of worms and insects are described. Competition amongst the organisms is important as limiting the output of the more offensive flies and also has some bearing on the behaviour of the filters. The advantages of the complete fauna in contrast to a restricted one are discussed and some factors which limit variety of forms are given. It is suggested that the grazing organisms deplete the active film below par in the warmer months, but the acceleration of the purification by higher temperatures largely compensates for this; therefore a general level of degree of purification by filters throughout the year results. Tested methods for the control of filter flies are listed.

Menzies, W. J. M. (1947). 'On the spawning of salmon: some observations of the process as seen from the Bridge o' Dee.' Salm. Trout Mag. (Lond.) no. 120: 130–2.

Description of mating behaviour of salmon (*Salmo salar*).

Reynoldson, T. B. (1941). 'The biology of the macro-fauna of a high-rate double filtration plant at Huddersfield.' Paper read to the north-eastern branch of The Institute of Sewage Purification on 15 March 1941. 16 pp.

The biology of an experimental high-rate filtration plant at Deighton was studied intensively and systematically over a period of 12 months. The primary bed (run at a high rate) and the secondary bed, studied as a partial control, are described. The primary bed was inoculated with some hundreds of *Psychoda* flies, and the number of macro-organisms were determined by systematic trappings throughout the period. Three separate methods for estimating fly abundance together with those of larvae were used. A comparison of the general bed conditions, and of the variability and abundance of the faunas of the primary and secondary beds is given. Species occurring were: Diptera: Psychodidae (*Psychoda alternata, P. cinerea, P. severini*) and Borboridae (mostly *Limosina* spp.); Coleoptera: Staphylinidae, Hydrophilidae (*Helophorus* spp., *Cercyon haemorrhous*); Oligochaeta: *Lumbricillus lineatus, Enchytraeus albidus*; Arachnida: spp. The abundance and distribution of *Psychoda alternata*, both flies and larvae, in the primary and secondary beds are described and compared. Differences in temperature affected the fly output of the beds. The relation between ponding and larval abundance is discussed. The main effects of the high filtration rate were a reduction of the variation of the fauna from ten to two breeding species and a reduction in the total abundance of the macro-fauna.

(*c*) Land

[Bootham School] (1946). 'Survey of Askham Bog.' London. 75 pp.

This survey follows one carried out in 1879 on the same area, and includes chapters on geology, botany, entomology, birds, invertebrates, an ecological report and general summary. Thirteen species of butterflies were identified during the summer of 1946; less attention was paid to the moth population, although the 1879 report included a list of 325 species. Five species of dragonflies were identified. Some 66 species of birds were seen in the area during 1946. The list is compared with that drawn up in 1879, and details of migratory and nesting activity are given. The short-eared owl (*Asio flammeus*) and the hen harrier (*Circus cyaneus*), were recorded in the earlier survey, but are not present now. Fifteen species of molluscs, three crustaceans, and ten further species of insects were identified. Only five species of mammals and two amphibians were recorded. A description of the plant associations and an attempt to divide the area into ecological units, together with a classification of the food-types among the animals, concludes the survey. [This area has recently been recommended by a government committee as a National Nature Reserve.]

Boyd, A. W. (1946). 'Early natural history records in Cheshire and South Lancashire.' Northw. Nat. 21: 50–7.

This paper, which is to be continued, contains records of mammals, birds and reptiles given in general surveys from 1086 to 1700, and of eight mammals and a reptile, classed as vermin, in churchwardens' accounts during the seventeenth to nineteenth centuries.

Cunliffe, N. & Hodges, D. J. (1946). 'Studies on *Oscinella frit* Linn. Notes on the resistance of cereals to infestation.' Ann. Appl. Biol. 33: 339–60.

Resistance of the oat plant is not correlated with either the carbohydrate or silica content. It is inferred that resistance is indirect and due to some form of attractiveness which determines the extent of oviposition because a variety resistant in the field can be rendered more susceptible than the most susceptible type by increasing the number of eggs placed on it. Oviposition in the field supports this view. Fly orientation is not controlled by chemotaxis or hydrotaxis but is influenced by stereotaxis. The resistance of Summer variety and of Victory to stem infestation in the spring is not extended to the grain infestation, no marked difference being observed.

Dixon, F. (1946). 'A rare spider in North Lancashire.' Northw. Nat. 21: 100–1.

Two mature females of *Dysdera erythrina* were taken in a house at Grange-over-Sands in April 1946. This is the most northerly record from Great Britain of this rare species.

Ellenby, C. (1946). 'The influence of potato variety on the cyst of the potato-root eelworm, *Heterodera rostochiensis* Wollenweber.' Ann. Appl. Biol. 33: 433–46.

There are significant differences in the response to the root excretions from four potato varieties and in the number of larvae emerging from the different cyst types on the same four potato varieties. The number of eggs in each cyst was determined. For each cyst type a constant proportion of eggs hatched. It is suggested that the differences in cyst size and egg number may be due to differences in the seasonal behaviour of the different potato varieties; differences in the hatching response of the cysts may then be due to the fact that the eelworm cyst responds to root excretions as a unit and that egg concentration is a factor affecting the nature of the unit.

Ellison, N. F. (1946). 'Unusual nest of turtle dove.' Northw. Nat. 21: 95.

A nest of *Streptopelia turtur* constructed of short lengths of insulated copper wire and rimmed with wire-netting was found at Kidderminster. Other records of the use of wire for nest-building by birds believed to be turtle-doves and by herons and greenfinches are quoted.

Gough, H. C. (1946). 'Studies on wheat bulb fly (*Leptohylemyia coarctata* Fall.). I. Biology.' Bull. Ent. Res. 37: 251–71.

Eggs hatch in January and early February. Severe frosts delay hatching but do not kill the eggs. The eggs also survive prolonged flooding. Oats are not a suitable host plant and though a few plants were infested the larvae did not survive. When two larvae infest the same wheat shoot one dies. The larvae leave the plants in April or early May and pupate in the soil. The pupal stage lasts 6–7 weeks. The flies emerge in June. Copulation takes place 3 weeks later, when dense aggregations of the flies occur. Usually males predominate in and occasionally comprise the entire aggregations. The females start egg-laying about a month after emergence. In Yorkshire this takes place in July and August and lasts about a month. Local variations in dates take place, lateness being associated with heavy soils.

Jackson, H. R. (1937). 'The Birds of Atholl.' Trans. Perthsh. Soc. Nat. Hist. 9: 173–81.

Notes on species of birds observed in Atholl with records of nestings; for May and June only.

Lancum, F. H. (1946). 'Wild birds and agriculture: 9. The house-sparrow.' J. Minist. Agric. 53: 415–16.

Lancum, F. H. (1947). 'Wild birds and agriculture: 10. The plovers.' J. Minist. Agric. 53: 459–61.

The lapwing (*Vanellus vanellus*) and golden plover (*Pluvialis apricarius*).

Lancum, F. H. (1947). 'Wild birds and agriculture: 11. The starling.' J. Minist. Agric. 53: 506–8.

Lancum, F. H. (1947). 'Wild birds and agriculture: 12. Some general reflections.' J. Minist. Agric. 53: 562–5.

Langmead, L. B. (1946). 'Land and freshwater Mollusca of the Tunbridge Wells area.' S.-East Nat. 51: 50–2.

The distribution of the 70 or so species of molluscs found within a radius of Tunbridge Wells is briefly discussed. Soil alkalinity is considered the chief factor in limiting the distribution of most species. Notes are added on the dispersal of various species through the agency of man.

McMillan, N. F. (1946). 'Cheshire conchological notes.' Northw. Nat. 21: 103–4.

Contains a list, with indications of abundance, of nine molluscs found on an old sandstone wall in April 1945 and distributional records for three others, two of which (*Caecilioides acicula* and *Helicella caperata*) are stated to be rare in Cheshire.

Massee, A. M. (1946). 'Notes on some interesting insects observed in 1945.' Rep. E. Malling Res. Sta., 1945 (33rd year): 90–5.

Notes and observations on 21 insect pests and mites noted in 1945, several of them noted for the first time.

Richardson, A. (1946). 'A supplement to Donovan's catalogue of the Macrolepidoptera of Gloucestershire.' Proc. Cotteswold Nat. Fld. Cl. 29: 76–107.

A list of the Macrolepidoptera of Gloucester which comprises 635 species including 75 new to the area. Notes are given on the relative abundance of the different species in recent years.

Sibson, S. B. (1946). 'Notes on birds of Sandbach, S.E. Cheshire.' Northw. Nat. 21: 58–67.

Notes on the distribution and status of 70 species are given in this concluding part.

Waddington, L. G. F. (1946). 'Occurrence of *Gastropacha quercifolia* Linn. in Yorkshire and North Notts.' Northw. Nat. 21: 101.

The lappet moth was recorded for the first time in the Doncaster district in July 1945 and from two places in north Nottinghamshire in June 1946; it has not been captured in either county in recent years. Larvae of *Lasiocampa quercus*, which is usually associated with moorlands, were found on a hawthorn hedge in Nottinghamshire.

Watson, J. M. (1944). 'IV. Studies on the morphology and bionomics of a little known holotrichous ciliate—*Balantiophorus minutus* Schew. Part 11.—The effect of environmental factors.' J. R. Micr. Soc. 64: 31–67.

Describes the movements and feeding mechanism. Experiments show that the ciliate is well adapted to life in the soil. The limits and optima of temperature and *p*H concentration at which multiplication will take place are given. It can survive anaerobic conditions for 3 weeks but high concentrations of CO_2 are fatal. The division rate is increased on exposure to light. It can move in an almost amoeboid fashion and can survive desiccation of its medium provided it is in contact with some moisture-retaining substance. Anabiosis, resulting in an unencysted resting stage, and encystation are described.

(*d*) Small islands

Bailey, J. H. & Britten, H. (1946). 'The Coleoptera of the Isle of Man.' Northw. Nat. 21: 68–71.

Contains corrections and additions and concludes series.

Bassindale, R. (1946). 'Studies on the biology of the Bristol Channel. XVI. The fauna of Skomer Island. A preliminary sketch.' Proc. Bristol Nat. Soc. 27: 109–20.

The fauna of Skomer Island is briefly described; particular reference is made to the intertidal fauna and flora. The shores of the island are rocky, and it is suggested that collections accompanied by observations on boulder size and wave action might yield information on the habitat requirements of different species.

Harrison, J. W. Heslop (1946). 'Noteworthy Lepidoptera from the Isle of Rhum with some notes on insects captured on the adjacent islands.' Entomologist, 79: 147–51.

Habitat and locality notes on 96 species of Lepidoptera.

2. GENERAL REPORTS AND TAXONOMIC STUDIES OF USE TO ECOLOGISTS

Ford, E. (1946). 'Vertebral variation in Teleostean fishes. III. Isospondyli.' J. Mar. Biol. Ass. U.K. 26: 390–7.

Both 'marker' characters and precise statistical characters in the backbones of Isospondylid fishes can probably be used in identifying different biological populations of the same species.

Southern, H. N., Watson, J. S. & Chitty, D. (1946). 'Watching nocturnal animals by infra-red radiation.' J. Anim. Ecol. 15: 198–201.

By means of infra-red radiation and a special telescope it is now possible to make continuous observations on nocturnal species, which generally have poor sensitivity to light of the longer wave-lengths. This technique has been successfully used to study and photograph the brown rat (*Rattus norvegicus*).

3. PARASITES

Day, C. D. (1946). 'British Tachinid Flies. Tachinidae (Larvaevoridae).' Northw. Nat. 21, Suppl.: 1–32.

In his introduction, the author states that this key deals with 160 genera arranged in 36 artificial primary groups for each of which dichotomous keys separating the genera are provided and that keys to the species, including indications of the abundance, habitat, period of occurrence, hosts, and flowers visited, follow each genus where it is small or are given separately where it is large; a key and 12 dichotomous tables of wing features, with 149 wing venation figures covering all the British genera supplies an additional means of identification. The rest of this paper comprises the keys to the primary groups and generic keys to two of them, with definitions and explanations of the morphological characters and terms employed and notes on the collection, preservation, examination and identification of Tachinids.

Edwards, E. E. & Arthur, D. R. (1947). 'The seasonal activity of the tick, *Ixodes ricinus* L., in Wales.' Parasitology, 38: 72–85.

There are usually two peaks of female activity in South Wales, one in spring and the other in autumn. The seasonal activity of nymphal and larval forms is essentially comparable to that found in the north of England. Significant differences in the mean populations of ticks on different breeds of cattle were not found.

Milne, A. (1947). 'The ecology of the sheep tick, *Ixodes ricinus* L. Some further aspects of activity, seasonal and diurnal.' Parasitology, 38: 27–33.

Tick activity curves for various animals, mammals and birds, are similar in form and timing. Where spring activity occurs, males, females and nymphs usually have similar and concurrent activity curves, but nymphs may occasionally have their peak 2–3 weeks later. Larval activity is always later, the peak being several weeks after the female peak.

Milne, A. (1947). 'The ecology of the sheep tick, *Ixodes ricinus* L. The infestations of hill sheep.' Parasitology, 38: 34–50.

In general, female ticks infest the hairy areas of sheep (head and legs); the comparatively bare areas (axillary and inguinal), and certain short-woolled areas (margins of hairy and bare areas); they do not attack in long-woolled areas. The average totals of female ticks carried per annum by ewe, hog and lamb were in the proportions of 8:6:1. Host size is thought to be the chief governing factor. The upper limits to female tick infestation appear to be of the following order: average spring peak total count per ewe reaches 100–150 and about five times as many ticks are carried per ewe over the entire spring season. In any age group of sheep on one grazing there is considerable but constant range in weekly infestation rates and the most important factor determining the level of infestation of a sheep is probably individual activity, i.e. the more ground covered in unit time, the more ticks picked up.

Wright, D. W. & Geering, Q. A. (1947). 'Pea moth.' J. Minist. Agric. 54: 124–9.

Parasites of *Laspeyresia nigricana* recorded in Cambridge and the Harlow district of Essex are *Ascogaster quadridentatus*, *Glypta haesitator* and *Hemiteles ridibundus*. Two wild vetches, *Lathyrus pratensis* and *Vicia cracca*, are recorded as alternate host plants.

4. FOOD AND FOOD HABITS

Glegg, W. E. (1947). 'Birds as the food of fishes.' Essex Nat. 28: 12–16.

A short account of a number of instances in which carnivorous fish have been observed to have eaten birds. Particular attention is paid to the predation of pike on young waterfowl.

Lack, D. (1946). 'Competition for food by birds of prey.' J. Anim. Ecol. 15: 123–8.

Among German hawks and owls, no two congeneric species compete for food in the same habitat. No two species from different genera compete for the same food supply, with the apparent exception of the predators on *Microtus arvalis*. This vole forms the staple food of several hawks and owls, of which up to five (none congeneric) may occur together in the same habitat. It is suggested that these predators do not effectively compete with each other because for most of the time *Microtus* is superabundant, while, when there is a vole minimum, each predator perhaps turns to different prey. Parallels are cited with other foods which are temporarily superabundant and the observations are briefly related to theories of population interaction.

Littleboy, C. G. (1947). 'The rook (*Corvus frugilegus*).' Rep. Rugby Sch. Nat. Hist. Soc. 80: 23–34.

Observations on a rookery, experiments with captive birds and a report of stomach content analyses. An interesting experiment on colour vision is described. A lamp and a prism were set up to throw a spectrum on a floor sprinkled with corn. Corn in the blue and violet light was left untouched, while in the red, green and yellow regions all of the corn was taken. On the basis of the examination of the stomachs of 100 birds taken at all times of the year it is concluded that the rook may be termed a beneficial bird.

Rowett, H. G. Q. (1946). 'A comparison of the feeding mechanisms of *Calma glaucoides* and *Nebaliopsis typica*.' J. Mar. Biol. Ass. U.K. 26: 352–7.

A benthic nudibranch and an abyssal crustacean both apparently adapted for seasonal feeding on fish eggs and for storing this food during the period when eggs are not available. The absence of an anus in *Calma*, and the extremely narrow gut of *Nebaliopsis* are probably associated with this almost completely digestible diet.

Thompson, R. W. S. (1946). 'The biology of Ladybower Reservoir.' The Institution of Water Engineers. London. Pp. 69–96.

An account is given of a series of observations made from April 1943 to the end of 1944 during the first filling of the reservoir. Measurements were made of chemical and physical data, and of the quantities of water released from the reservoir; these are presented in diagrammatic form. Planktonic Entomostraca and Rotatoria were found to occur in abundance throughout most of the year, despite the relative paucity of the flora (caused probably by the large-scale replacement of the water by inflow and outflow). It is concluded that the abundance of these animals was chiefly caused by the decay of submerged grass, and that planktonic algae did not form a very large part of their food. A rough estimate of the total bulk of some of the planktonic organisms and fish suggests that the phytoplankton, even when most abundant, was not enough to form a large proportion of the food of the animal forms. The maximum gross bulk of one of the latter, *Daphnia longispina*, however, was greater than that of the fish, which fed extensively on it. Some particulars are given of the growth of trout (*Salmo trutta*) in this reservoir, and of their summer food. *Daphnia*, chironomid larvae and pupae were found to be the main foods, but other aquatic and terrestial insects were being eaten in fair quantities. A relatively high growth rate was observed for the trout, principally due to the submergence and decay of vegetation. An account of a discussion and written contributions following the paper is included.

Wilson, D. P. (1946). 'A note on the capture of prey by *Sepia officinalis* L.' J. Mar. Biol. Ass. U.K. 26: 421–5.

By aquarium observations and the analysis of photographs, the hunting behaviour of *Sepia* is described. Usually the approach is stealthy, or it lies in wait for a victim, so that the element of surprise is important. A crab or prawn which is aware of the *Sepia* appears to make ready to dodge the tentacles when these are shot out. In the sea no doubt the prey sometimes escapes. A hungry *Sepia* will actively chase its prey.

5. POPULATION STUDIES

Broadbent, L. (1946). 'A survey of potato aphides in north-west Derbyshire, 1945.' Ann. Appl. Biol. 33: 360–8.

Counts of aphides infesting potato crop at altitudes between 340 and 1360 ft. Peak figures reached over 1500 per 100 lower leaves. In many fields two peaks were noted, one towards the end of July and the second in mid-September. Sheltered fields were the least infested. No evidence was obtained to show that altitude and aspect of the field influence the intensity of infestation.

Cockbill, G. F., Ross, D. M. & Stapley, J. H. (1947). 'Wireworm populations in relation to crop production. III. Population changes after summer ploughing.' Ann. Appl. Biol. 34: 83–94.

Six permanent pastures broken up in the summer of 1943 were sampled once a fortnight after ploughing. On four of the fields, a slight increase in *Agriotes* populations was apparent up to December followed by a decline in February and March. On two fields, the counts declined by about 30% during the autumn and winter. A marked fall in population (30–70%) was evident on all fields only after the first crop had been harvested. The decline in population during the autumn and winter is due to the ploughing, but that in the spring and summer normally occurs in grassfields. However, that, after summer ploughing, is permanent.

Ellison, N. F. & Wilson, W. (1946). 'Kestrel breeding on Hilbre Island, Cheshire.' Northw. Nat. 21: 95.

Falco tinnunculus bred, evidently for the first time, on Hilbre Island in 1945, when five young birds were reared. It is increasing as a nesting species in the Wirral.

Harting, A. Mayr- (1947). 'The growth of bacterial colonies and their viable population.' J. Hyg., Camb. 45: 19–27.

Colonies of *B. coli* were grown on an agar culture. It was found that the maximal population reached by a colony is dependent on the number and distance of neighbouring colonies. It is higher the less colonies there are in the culture and the greater the distance between them. The time when the maximal viable count is reached depends on the same factors and the sum of the theoretically calculated maximal viable counts of all colonies is equal per area of culture surface. The relationship of the results to those obtained in liquid media is discussed.

Hickling, C. F. (1946). 'The herring fisheries of Milford Haven.' J. Mar. Biol. Ass. U.K. 26: 408–20.

At Milford Haven there are three herring (*Clupea harengus*) fisheries: a winter drift-net fishery, a spring drift-net fishery, and a trawl fishing in summer and autumn. Samples from these fisheries show a continuous change in the condition of the gonads, so that the catches may all be from the same stock. A correlation exists making it possible to forecast the summer and autumn fishing prospects from the statistics of the spring drift-net fishery. There is no evidence that the phases of the moon influence the Milford Haven fishery, except in September when a statistical correlation exists between a bad catch and a full moon in the first half of the moon.

Hickling, C. F. (1946). 'Haddock on the Porcupine Bank, September 1944.' J. Mar. Biol. Ass. U.K. 26: 398–407.

The haddock (*Gadus aeglifinus*) population of the Porcupine Bank is probably a self-contained stock. There was no fishing on the bank between 1940 and 1944, and the stock increased to some five times its pre-war density. Contrary to expectation, the slowing of the growth rate, due to a supposedly intensified competition for the available food, seems not to have occurred in this population.

Hutton, J. A. (1947). 'Wye salmon, 1946: Report of the Wye Board of Conservators.' Salm. Trout Mag. (Lond.) no. 120: 159–72.

The total catch of salmon (*Salmo salar*) was 2891 fish weighing 41,965½ lb. Of these, only 481 were taken by net. A poor season, with deficiencies in all classes of fish except grilse.

Hutton, J. A. (1947). 'Salmon scarcity: an attempt to get the real facts.' Salm. Trout Mag. (Lond.) no. 119: 55–62.

A criticism of the theory of a cyclical periodicity in salmon (*Salmo salar*) runs.

Morley, D. W. (1946). 'The interspecific relations of ants.' J. Anim. Ecol. 15: 150–4.

Wheeler's classification of the mixobiotic colonies of ants is criticized on the grounds of its purely descriptive basis, and its incompleteness. A more comprehensive systematic classification based on behaviour is presented. Two main categories of interspecific relations, casual and obligatory, are further divided into tolerant and competitive relationships. A description of each type of relationship is given, with examples illustrating them. Myrmecophilous relationships can be dealt with under the same system.

Roebuck, A. (1946). 'Notes on the economic zoology of Lincolnshire during 1945.' Trans. Lincs. Nats. Un. 11: 134–7.

Notes dealing with pests which attacked commercial crops. Includes comments on extent of damage and the use of D.D.T.

Ross, D. M., Stapley, J. H. & Cockbill, G. F. (1947). 'Wireworm populations in relation to crop production. II. Population changes in grassland.' Ann. Appl. Biol. 34: 66–82.

Six grass fields were sampled once a fortnight from July 1943 to September 1944, the wireworms (*Agriotes*) being counted by the washing and flotation method. Minimum populations in July and August, rising populations throughout the autumn, maximum populations in the months from January to April, followed by a sharp decline during April to July. The winter numbers were on the average twice as high as those in summer. The fluctuations were most marked in the wireworms 'under 4 mm.', '4 mm.' and '5 mm.' On the average 75% of the wireworms were in the 0–6 in. layer and about 90% in the 0–12 in. layer. These proportions varied with the season. These seasonal changes in wireworm populations do not correspond with those expected from the life history of *Agriotes* species. This is discussed.

Southern, H. N. & Laurie, E. M. O. (1946). 'The house-mouse (*Mus musculus*) in corn ricks.' J. Anim. Ecol. 15: 134–49.

Counts of mouse-holes in the sides of ricks show that in wheat there is a fairly constant relation between the number of holes and number of mice. Badly infested ricks may contain from 1·4 to 14 mice per cu.m. These populations show a rapid rate of occupation of ricks in the autumn, and by January over 90% of ricks are infested. The size of population rises rapidly after the rick has been built, reaching a peak in the spring; after a rick is eight months old there is little if any increase in the mouse population. The movements of the mouse populations are described: the species was found to be the third commonest small mammal living in the fields. Damage can be estimated roughly by the percentage of 'tailed' (broken) corn in the total yield at threshing.

Stapley, J. H., Ross, D. M. & Cockbill, G. F. (1947). 'Wireworm populations in relation to crop production: IV. Population changes during a bare fallow.' Ann. Appl. Biol. 34: 95–103.

Twenty-three fields were studied in 1943 and 1944. In such fallow fields *Agriotes* populations were much reduced, sometimes to less than 10% of the original. All sizes of wireworms were affected, particularly those less than 5 mm. in length. The decline cannot be wholly attributed to the bare fallow since the grass 'controls' also declined during the same period. The decline is different in so far as after fallow it is permanent and continues through the autumn when the counts in the 'controls' are rising.

Went, A. E. J. (1946). 'Salmon of the River Shannon in 1944 and 1945.' J. Anim. Ecol. 15: 155–69.

The age distribution of the salmon (*Salmo salar*) captured in the River Shannon in 1944 and 1945 and the mean sizes and condition coefficients of the various age groups in 1945 were calculated. The proportion of the total catch filled by different age groups is given. Records of catches for 1927–45 show that since the start of the hydro-electric scheme there has been a considerable reduction in the numbers of fish which have spent two or more years feeding in the sea. The total catch in 1941 was about 60% less than in 1928. Numbers of grilse have remained roughly constant since 1927. Ways in which the construction of the hydro-electric plant has affected the salmon are discussed.

Went, A. E. J. (1946). 'The Irish pilchard fishery.' Proc. R. Irish Acad. 51, B, no. 5: 81–120.

An historical account of the industry pilchard (*Sardina pilchardus*) from 1611 to 1944, with a list of 'pilchard years' between these dates. The fluctuations are quite irregular. The shoals are mainly distributed round the south coasts of Ireland.

Went, A. E. J. (1947). 'Value of the kelt: some notes on previously spawned salmon in Ireland.' Salm. Trout Mag. (Lond.) no. 119: 41–8.

Most salmon (*Salmo salar*) die after spawning once. In Irish rivers the proportion surviving varies, it is suggested according to the intensity of fishing. Previously spawned fish are sufficiently numerous to be commercially valuable and should be conserved.

6. MIGRATION, DISPERSAL AND INTRODUCTIONS

Anon. (1947). 'The fight against Colorado beetle, 1946.' J. Minist. Agric. 54: 121–4.

Record of occurrences of *Leptinotarsa*, including a distribution map.

Fraser, F. C. (1946). 'Report on Cetacea stranded on the British coasts from 1933 to 1937.' British Museum (Nat. Hist.) Report on Cetacea, No. 12: 56 pp., 11 figs., 7 maps.

Since 1927–1932 there have been increased strandings of the common porpoise (*Phocaena phocaena*), common dolphin (*Delphinus delphis*) and false killer whale (*Pseudorca crassidans*). The sperm-whale (*Physeter catodon*) and common dolphins stranded in 1937 are attributed to the invasion of the North Sea by the squid *Todarodes sagittatus* in that year. The white whale (*Delphinapterus leucas*), formerly reported, is absent, but the British Isles represent the extreme southern limit of its range. No rorquals (*Balaenoptera*) were identified and this may be the effect of whaling in the past years.

Rankin, M. N. (1946). 'The autumn migration (1945) in the North Sea.' Northw. Nat. 21: 98–100.

A list is given of some 23 species of birds observed over the southern North Sea between the middle of August and early November, with indications of numbers and behaviour.

Small, T. (1947). 'Colorado beetle in Jersey, 1939–46.' J. Minist. Agric. 53: 450–3.

An account of the outbreaks of *Leptinotarsa* since the initial discovery on 3 October 1939.

Taylor, W. L. (1946). 'The wild cat (*Felis silvestris*) in Great Britain.' J. Anim. Ecol. 15: 130–3.

In recent years the wild cat has increased its range and numbers in northern Scotland. A map and table of the occurrence of the species in the Forestry Commission areas in Scotland are given.

The Yorkshire Fishery Board (1946). 'History and report on fish passes and migratory fish in the Yorkshire Fishery Board's Area.' 27 pp.

The history and legal position of the Board is described. The average weight per year of salmon (*Salmo salar*) and migratory trout (*S. trutta*) caught in the area taken in 15-year periods from 1867 to 1944 shows a marked decrease. Some causes of the decline are discussed, and measures for improvement are suggested. A history and description of the weirs, obstructions, and fish passes on the Ouse and its tributaries (with the exception of the Aire, Don, and Calder) accompany the report.

7. REPORTS OF ORGANIZATIONS

Blundell's School Science Society. Magazine (1946). No. 1. 51 pp.

Short papers include: the ecology of a stream on Exmoor, butterfly records for the Tiverton area in the summer of 1946, the fauna of a swiftly flowing stream in Eppscleave wood, an ecological study of a sea pool, the food of the wood-pigeon during spring 1946 in the Camborne-Redruth area, and the food of the stoat and its effect on other animals in the district of Burrington Combe.

Jane, F. W. (1946). 'The natural history of Hertfordshire.' Trans. Herts. Nat. Hist. Soc. Fld. Cl. 22: 142–59.

An analysis of the work that has been done on the county flora and fauna. The writer emphasizes the desirability of continued observation so that both quantitative and qualitative fluctuations in the flora and fauna may be recorded. Annual reports for 1945 are given in *ibid.*: pp. 114–24 (birds, by H. H. S. Hayward); pp. 125–9 (Lepidoptera, by A. H. Foster); p. 129 (Mollusca, by A. E. Salisbury).

Oundle School Natural History Society. Annual Report (1947). 31 pp.

A list of dates for 1945 and 1946 is given for the first observation of spring migrant birds and also for Lepidoptera. In 1946 the wainscot moth, *Arenostola extrema*, was seen locally. A complete list of local birds is given, to replace the 1938 list. A local heron census showed a continued decline in numbers. Notes for 26 bird species are given for the period 1945–6.